# Life-history and population dynamics of the range extending *Octopus tetricus* (Gould, 1852) in south-eastern Australia

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(B. Mar. Biol., M. Sc.)

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for the degree of Doctor of Philosophy in Natural and Physical Sciences

Institute for Marine and Antarctic Studies
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## Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

15 August 2015

Jorge Eduardo Ramos Castillejos Date

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Paper 4 (in preparation), based on Chapter 4:
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Gretta T. Pecl Date

**Abstract**

Ocean warming may impact the physiology, morphology, or behaviour of marine organisms that are already living close to their limits of thermal tolerance. In response to warming, many marine species are contracting, relocating or extending their geographic range in order to keep pace with their preferred thermal environments. However, variation in the magnitude of range shift responses to ocean warming is great and the mechanisms behind those range shift responses are poorly understood. Most of our understanding on how life history characteristics and population dynamics relate to range shifts is based on studies on terrestrial or marine invasive species but these may differ from climate-driven marine range shifting species. Moreover, examining climate-driven marine range shifts of long-lived species is challenging. The use of short-lived marine range-shifting species may thus facilitate examining how life history characteristics and population dynamics relate to climate-driven marine range shifts, which may allow us to increase our capacity to anticipate changes in species distributions, assess their potential impacts, and develop appropriate management strategies. In the southern hemisphere, *Octopus tetricus* (Gould, 1852) has undergone a recent polewards range extension from southern Queensland and New South Wales into Victorian and Tasmanian waters, likely associated with the strengthening of the East Australian Current. Therefore, this study investigated how life history characteristics, population dynamics and genetics may relate to the rapid range extension of *O. tetricus*.

In Tasmanian waters, *Octopus tetricus* had a maximum total weight of 2.3 kg, demonstrated fast growth rates and a short lifespan of approximately 11 months. Temperature, food availability, and gender appeared to influence growth rate. Individuals that hatched during cooler and more productive conditions, but grew

during warming conditions, exhibited faster growth rates and reached smaller body sizes than individuals that hatched into warmer waters but grew during cooling conditions. Fast growth and the associated rapid population turnover may provide an advantage over longer-lived native species, facilitating the range extension of *O. tetricus*. Mature females with developing eggs were found off north-eastern Tasmania. Fecundity was high and more mature females were observed during the austral spring and summer compared to other seasons of the year; the reproductive cycle of females thus seemed to be timed to favourable seasonal environmental conditions, whereas mature males were observed all year round. Females matured later and had larger body size at maturity compared to males. *Octopus tetricus* has the capacity to reproduce in the new parts of its range and the population has the potential to be self-sustainable, which may enable the size of the emerging population to increase at the extended zone. The population at the range extension zone was sub-structured with a distinct group predominately comprised of individuals from Tasmania. Genetic diversity within the range extension zone was maintained compared to the historical distribution area. The range extension of *O. tetricus* is likely to be facilitated by high and constant dispersal of paralarvae, high gene flow from a diversity of source areas, and high genetic diversity. These features would favour adaptation to new environments and facilitate establishment beyond the historical geographic limits, potentially allowing *O. tetricus* to prevail at the range extension areas. These results suggest that fast growth rate, rapid population turnover, high reproductive capacity, synchronization with favourable environmental conditions, high gene flow from a diversity of source areas, and high genetic diversity are some of the enabling factors that may allow the establishment and prevalence of the population of *O. tetricus* in the range extension zone.

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# Chapter 1

## General introduction

Parts of this chapter formed my contribution to the following publication:

Rodhouse PGK, Pierce GJ, Nichols OC, Sauer WHH, Arkhipkin AI, Laptikhovsky VV, Lipinski MR, **Ramos JE**, Gras M, Kidokoro H, Sadayasu K, Pereira J, Lefkaditou E, Pita C, Gasalla M, Haimovici M, Sakai M, Downey N (2014) Environmental effects on Cephalopod population dynamics: Implications for management of fisheries. In: *Advances in Marine Biology. Advances in Cephalopod Science: Biology, Ecology, Cultivation and Fisheries*. Vol. 67, Vidal EAG (editor). pp 140–145. Academic Press, London

# Chapter 1. General introduction

## 1.1 Ocean warming and the south-east coast of Australia

Human activity has accelerated the natural rate of change in the climate resulting in acute oceanic changes (United Nations Framework Convention on Climate Change 2012). The most evident change in the climate is the warming of the oceans, which has accelerated from the 1950s (Levitus *et al*. 2012). Oceanic hotspots are regions where surface temperatures changed rapidly over the past 50 years and are projected to continue to change at a rapid rate into the future (Hobday & Pecl 2014). One of these hotspots is located along south-eastern Australia and has been associated with the strengthening further south of the East Australian Current (EAC) (Ridgway 2007; Hill *et al*. 2008; Hobday & Pecl 2014). The EAC is the major western boundary current of the South Pacific sub-tropical gyre that flows from the southern Coral Sea and reaches the south-east coast of mainland Australia (Ridgway & Dunn 2003). Over the past 60 years, the EAC has extended approximately 350 km south, penetrating further along the relatively cool east coast of Tasmania (Fig. 1.1) (Ridgway 2007; Hill *et al*. 2008). Consequently, the recent rate of warming in south-east Australia is up to four times greater than the global average, and ocean temperatures in the region are projected to increase by 3°C by 2070 (Poloczanska *et al*. 2007; Hobday & Pecl 2014).

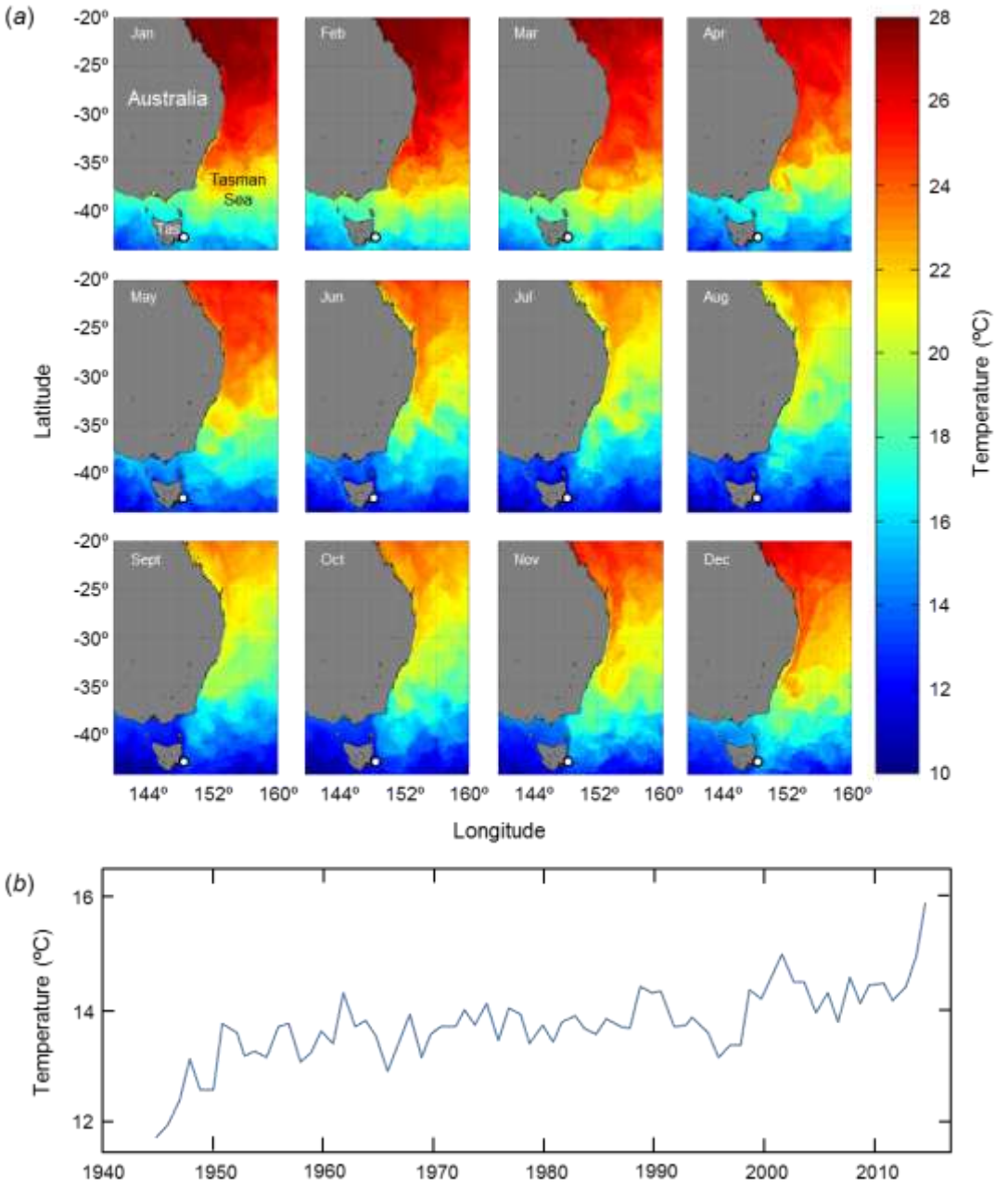


Figure 1.1 Oceanic warming along the east coast of Australia. (*a*) Extension of the warm East Australian Current throughout 2006, a year when the common Sydney octopus *Octopus tetricus* was detected for the first time off north-eastern Tasmania; (*b*) Sea surface temperature recorded from 1944 to 2014 at the Maria Island Time Series station off the south-east coast of Tasmania at 42.6°S, 148.23°E on the 50 m isobath. The location of the Maria Island Time Series station is indicated with a white circle on the top panel

## 1.2 The climate-driven range shift framework

Ocean warming may mainly impact the physiology, morphology, and behaviour of marine organisms that already live close to their limits of thermal tolerance (Somero 2002; Harley *et al*. 2006). In response to ocean warming many marine species are consequently shifting their distributions to occupy preferred thermal environments (Parmesan & Yohe 2003; Sunday *et al*. 2012; Pinsky *et al*. 2013). A range shift is the change in the distribution of native species from their previously recorded boundaries, whether the range contracts, relocates or extends (Fig. 1.2) (Madin *et al*. 2012). A range extension consists of three successive stages: 'arrival', 'population increase', and 'persistence' in space and time (Bates *et al.* 2014). 'Arrival' is initiated by the presence of individuals in a new geographic region. 'Population increase' occurs via self-recruitment and/or constant migration; and 'persistence' takes place when range extending populations remain geographically stable in the zone of extension (Bates *et al.* 2014).

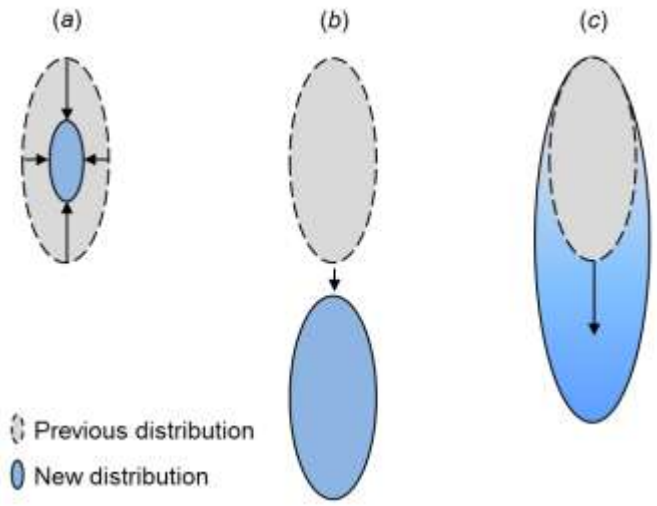


Figure 1.2 Schematic representation of range shifts. (*a*) Range contraction, the range of distribution is reduced and limited to one or several areas within the historical distribution; (*b*) Range relocation, the distribution of the population is entirely moved to another area; (*c*) Range extension, the historical distribution is extended to new areas (Based on Madin *et al.* 2012)

### 1.3 Life-history and population dynamics

Range shifts are in many ways analogous to the processes of invasion (range extension) and local extinction (range contraction) (Bates *et al.* 2014). Therefore, much of our knowledge on the factors that modulate the range extensions of species is based on the invasion ecology framework where the introduction, establishment, and spreading of non-native populations is modulated by the frequency and number of introduced individuals, the environmental conditions and the community interactions in the new areas (Colautti *et al*. 2006; Lockwood *et al.* 2007). If environmental conditions are not suitable and the availability of resources is limited at new areas, metabolic performance (Pörtner & Farrell 2008; Kearney & Porter 2009; Calosi *et al*. 2013), body size, age-class structure (Stenseth *et al*. 2002), timing of ontogenetic transitions and reproduction may be affected (Harley *et al*. 2006). Some of these life history characteristics (McMahon 2002; Amundsen *et al*. 2012), in addition to dispersal ability (Cowen & Sponaugle 2009; Travis *et al.* 2013), and intra and inter-specific interactions, among other factors (Colautii *et al.* 2006; Blois *et al.* 2013) are likely to play a role in the ability of climate-driven range shifting species to colonize new areas. At first glance, species with broad physiological tolerance, fast growth rates, rapid population turnover, high fecundity, generalist feeding habits, high dispersal ability, and which are already at their physiological limits are likely to be able to change their distribution and thrive in new environments. However, range shifts of species whose life history traits differ from the previous expectations also have been documented (Przeslawski *et al.* 2012; Bates *et al.* 2014; Sunday *et al.* 2015). Additionally, variation in the magnitude of the range shifts is considerable (Poloczanska *et al.* 2013; Sunday *et al.* 2015), and our understanding of what traits may allow species to establish and spread in new areas is poor. Therefore, it is

crucial to identify how life history characteristics and population dynamics relate to the capacity of species to undergo range shifts and prevail in new environments.

### 1.4 Population genetics

The range shift of species changes the spread of lineages across climate gradients, the origins of surviving lineages, and the sites of subsequent survival of those lineages (McInerny *et al*. 2009). Gene flow, genetic recombination, and selection against poorly adapted genotypes throughout a species range are critical for survival because they allow maintenance of the genetic diversity and the adaptive potential of populations (Davis & Shaw 2001; Hauser *et al*. 2002). Genetic diversity is expected to be greater in populations where the distribution experiences a wide variety of environmental conditions as individuals will be exposed to different environments. This may be reflected in populations that span a wide latitudinal distribution and that are favoured to undergo range shifts with success (Sunday *et al.* 2015). Once arrived in new areas, populations are exposed to demographic effects that may affect their establishment via reduction of genetic diversity. If a population undergoes bottle necks and its effective population size is reduced after the arrival in a new area, the population at the range extension zone is at risk of suffering genetic diversity depression (Austerlitz *et al*. 1997; Frankham *et al.* 2014). However, if individuals at the new areas are connected with individuals from a wide variety of environments at the historical distribution, the population has more possibilities to maintain genetic diversity and adaptive potential within the range extension area (Hauser *et al.* 2002). Population connectivity depends on oceanic currents (White *et al.* 2010), dispersal abilities or migration capacity, which allows reproductive exchange between individuals, facilitates gene flow and maintains genetic diversity

(Reichow & Smith 2001; Ray *et al*. 2003; Waples & Gaggiotti 2006). Therefore, examination of the population genetic structure, gene flow, and genetic diversity of a species that has undergone a range extension will aid in predicting if the range extending population will be capable of prevailing in the new areas.

### 1.5 Ecological and socio-economic impacts of climate-driven range shifts

In the last decades climate-driven changes in the distribution of phytoplankton, zooplankton, intertidal communities, fishes, and cephalopods, among others, have been documented in the Pacific Ocean (Holbrook *et al*. 1997; Sagarin *et al*. 1999; deYoung *et al*. 2004; Hatfield & Hochberg 2007), the North Sea (Nehring 1998; Beare *et al*. 2004), the Atlantic Ocean (deYoung *et al*. 2004; Richardson & Schoeman 2004), and the Mediterranean (Chisholm *et al*. 1995; Nieder *et al*. 2000). Such changes in distribution are expected to become more common with the accelerated warming of the oceans, and may result in community reorganization, changes in dominant species, and changes in ecological networks that modify the structure and function of ecosystems (Stenseth *et al*. 2002; Alheit & Niquen 2004; deYoung *et al*. 2004; Edwards & Richardson 2004; Alheit 2009; Walther 2010; Madin *et al*. 2012). Socio-economic impacts on fisheries, aquaculture/mariculture, tourism, health, and research are also expected (Madin *et al*. 2012). Therefore, it is important to investigate how life history characteristics, population dynamics and genetics, and evolutionary processes relate to the range shifts of marine species, and their prevalence in new areas. This may in turn permit identifying what species are most or least likely to undergo climate driven-range shifts and persist beyond their historical geographic limits. Integrating this knowledge could underpin the

development of appropriate management responses for the species detected to be undertaking range shifts, and for flow-on impacts to surrounding ecosystems.

### 1.6 *Octopus tetricus* as a case study

Long-term data sets appropriate for examining the response in life history parameters of long-lived species that undergo climate-driven range shifts are rarely available (Hoving *et al*. 2013). However, ecologically and commercially important cephalopods (Clarke 1996) may be ideal models to examine such life history parameters as a function of their generally short lifespan (Mangold 1983a). Many species of cephalopods are subjected to oceanic currents during their planktonic early stage of life or are capable of actively migrating large distances during the adult stage (see Hanlon & Messenger 1996 references therein; Sobrino *et al*. 2002; Boyle & Rodhouse 2005). Range shifts of cephalopods in response to environmental variability have already been documented in the Atlantic Ocean, e.g. *Argonauta argo*, *Illex argentinus*, *I. illecebrosus*, and *Todarodes sagittatus* (Guerra *et al*. 2002; Rodhouse 2008), and in the Pacific Ocean, i.e. *D. gigas*, *T. pacificus* (Zeidberg *et al.* 2007; Rodhouse 2008), and recently *Octopus tetricus* (Tasmanian Department of Primary Industries and Water 2009; Johnson *et al*. 2011; Robinson *et al.* 2015).

The gloomy octopus or common Sydney octopus, *Octopus tetricus* (Gould, 1852), is a merobenthic species with a maximum weight of 3 kg and total length of 80 cm (Roper *et al*. 1984; Rowling *et al*. 2010), with unknown life history characteristics and population dynamics. The historical distribution of *O. tetricus* along the east coast of Australia was from southern Queensland to southern New South Wales (NSW) (Edgar 2000; Norman & Reid 2000). However, the geographic distribution of *O. tetricus* has extended to south-eastern Australia, along the coast of

Victoria, where it was first detected after the year 2000 (Villanueva & Norman 2008; Edgar & Stuart-Smith 2014), and along the relatively cooler coast of eastern Tasmania where it was first detected in the year 2006 (Fig. 1.3) (Tasmanian Department of Primary Industries and Water 2009; Johnson *et al.* 2011; Edgar & Stuart-Smith 2014; Robinson *et al.* 2015). The range extension of *O. tetricus*, like many other range shifts in south-eastern Australia (Ling *et al*. 2009; Pitt *et al*. 2010; Johnson *et al.* 2011; Last *et al.* 2011), is thought to be related to the strengthening of the warm EAC (Ridgway 2007; Hill *et al.* 2008) via dispersion of paralarvae.

*Octopus tetricus* is commercially important in both the historical and, more recently, range extension areas. However in the historical range there is no information about its life history characteristics, population dynamics, or stock assessments (Rowling *et al*. 2010). Along the east coast of mainland Australia octopuses are caught throughout the year using fish or prawn trawl nets in <100 m (Nottage *et al.* 2007; Emery *et al.* 2014). In northern NSW prawn trawls of 40 mm mesh size are used, whereas the central and southern NSW fisheries use fish trawls of ≥90 mm mesh size (Nottage *et al.* 2007). *Octopus tetricus* usually comprises 20–40% of the commercial octopus catch in NSW (Nottage *et al.* 2007; Rowling *et al*. 2010). In Tasmanian waters *O. tetricus* contributes 14% of the commercial octopus catch, where octopuses are caught using unbaited black plastic pots (0.3-m long × 0.1-m high × 0.1-m wide) attached every ~5 m intervals to a 500 m line laid on the seafloor (<50m depth) for up to 30 days. Pots are weighted with concrete to minimise movement of the gear and the line has weights at both ends and a haul-in line and buoy attached to each weight.

*Octopus tetricus* feeds on crustaceans, and molluscs such as gastropods, bivalves, and other octopuses (Norman 2000; Norman & Reid 2000), and would

likely be able to out-compete other predators in the extended areas and displace resident species of octopuses (Villanueva & Norman 2008). *Octopus tetricus* could also cause extensive impacts via predation on other commercial species, i.e. predation by octopuses on trap-caught rock lobsters causes considerable financial losses to the fishery in Australia (Joll 1977; Brock & Ward 2004). The incursion of the common Sydney octopus into Victorian and Tasmanian waters may represent additional financial losses to the Southern rock lobster fishery and other fisheries. The likely ecological and economic implications of the range extension of *O. tetricus* beg for examining the capacity of this species to establish and prevail in range extension areas.

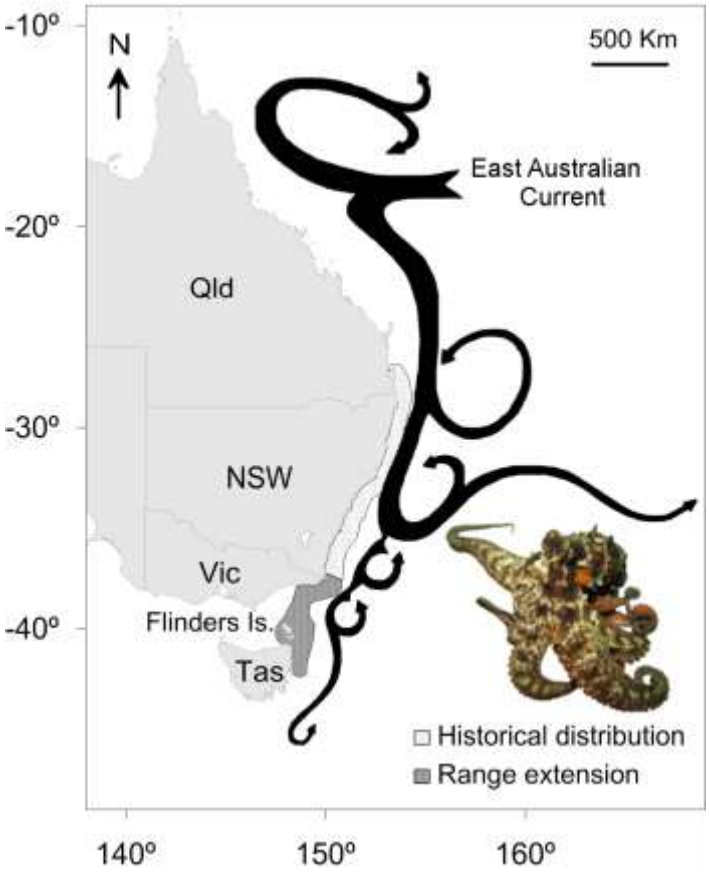


Figure 1.3 Distribution of *Octopus tetricus* along the east coast of Australia. The historical distribution is indicated in light grey and the range extension in dark grey. Qld, Queensland; NSW, New South Wales; Vic, Victoria; Tas, Tasmania. Photo of *O. tetricus* by Rick Stuart-Smith

## 1.7 Thesis aims and structure

The general aims of this thesis are to examine the life history traits and population dynamics of *O. tetricus* within the range extension area, and to study the population genetics throughout its range, with a focus on implications for populations within recently established regions. The information generated in this study may also assist in the management of this commercially important species.

This thesis is structured in five chapters (Fig. 1.4):

**Chapter 1.** The general introduction includes the background, identifies gaps in knowledge, and provides a general description of the species case study, as well as the approaches that are used to address the gaps in knowledge identified.

Parts of this chapter formed my contribution to the following publication: Rodhouse PGK, Pierce GJ, Nichols OC, Sauer WHH, Arkhipkin AI, Laptikhovsky VV, Lipinski MR, **Ramos JE**, Gras M, Kidokoro H, Sadayasu K, Pereira J, Lefkaditou E, Pita C, Gasalla M, Haimovici M, Sakai M, Downey N (2014) Environmental effects on Cephalopod population dynamics: Implications for management of fisheries. In: *Advances in Marine Biology. Advances in Cephalopod Science: Biology, Ecology, Cultivation and Fisheries*. Vol. 67, Vidal EAG (editor). pp 140–145. Academic Press, London

**Chapter 2.** Given the life history characteristics of cephalopods it was predicted that *O. tetricus* has fast growth rates and rapid population turnover, allowing *O. tetricus* to establish and rapidly increase the size of the population in the range extension areas. The stylets are the vestigial shell of octopuses in the form of paired hard structures found in the mantle; these structures have been used with success to estimate growth rates and age for octopuses (Doubleday *et al.* 2006; Barratt &

Allcock 2010), and aid the estimation of life span and population turnover. In this study I used the stylets as an ageing tool for *O. tetricus* to investigate how growth rates and population turnover may influence the capacity of this range extending species to establish in new areas.

This chapter was published as: **Ramos JE**, Pecl GT, Moltschaniwskyj NA, Strugnell JM, León RI, Semmens JM (2014) Body size, growth and life span: implications for the polewards range shift of *Octopus tetricus* in south-eastern Australia. *PLoS ONE 9*, e103480. doi: 10.1371/journal.pone.0103480

**Chapter 3.** Establishment of individuals in range extension zones requires the new environment to support their capacity to produce viable gametes and survival of offspring. The reproductive characteristics of *O. tetricus* have not been investigated along its distribution off eastern Australia and it is unknown if this species is capable of reproducing within the range extension area. The EAC brings warmer waters into south-eastern Tasmania; however, the historical distribution is warmer (annual average 20°C ± 0.2 s.e. at 32°31'15"S, 152°28'45"E) compared to the range extension area (annual average 15°C ± 0.2 s.e. at 39°33'45"S, 148°13'45"E). Cephalopods have extremely flexible life histories due to their response in growth to temperature, with slower growth rates at lower temperatures (Forsythe & Van Heukelem 1987; Forsythe 2004). Assuming that minimum temperature thresholds for growth and reproduction are met, the hypothesis of this study is that *O. tetricus* would mature relatively late at a large size, probably resulting in great potential fecundity in the cool waters of the range-extension area. Sex ratio, maturity, reproductive and somatic condition, size and age at maturity, and fecundity were thus examined for the first time at the extended area off south-eastern Australia. The

influence of reproductive characteristics of *O. tetricus* on its capacity to prevail and increase the size of the population at the range extension area is discussed.

This chapter was published as: **Ramos JE**, Pecl GT, Semmens JM, Strugnell JM, León RI, Moltschaniwskyj NA (2015) Reproductive capacity of a marine species (*Octopus tetricus*) within a recent range extension area. *Marine and Freshwater Research*. doi: 10.1071/MF14126

**Chapter 4.** Our understanding of the genetic structure and connectivity of range shifting populations and the evolutionary processes involved in range shifts is limited. Similar to invasive species, species that undertake range extensions usually experience a reduction in genetic diversity caused by a series of genetic bottlenecks along the range extension axis, or due to founder effects in the range extension area (Austerlitz *et al*. 1997; Hallatschek & Nelson 2010). Given the apparently recent range extension of *O. tetricus*, it is predicted that this species has not experienced population subdivision, but it may have reduced in genetic diversity in the range extension area compared with the historic range. To test these hypotheses, the population genetic structure, gene flow, and genetic diversity, among other genetic attributes of the population of *O. tetricus* at the historical and range extension areas along eastern Australia were examined using microsatellite markers. Microsatellites markers are informative at the population level in octopuses (Doubleday *et al*. 2009; Strugnell *et al.* 2012) and may allow investigation of how these genetic signatures relate to the capacity of *O. tetricus* to prevail in new areas.

This chapter will be submitted as: **Ramos JE**, Pecl GT, Semmens JM, Moltschaniwskyj NA, Souza CA, Strugnell JM. Population genetic signatures of a recent marine range extension

**Chapter 5.** This is a general discussion that synthesizes findings from all data chapters (Chapters 2 to 4). This chapter discusses how each factor examined influences the climate-driven range extension of *O. tetricus*. Suggestions are made on other life history traits, biotic, and abiotic factors that were not examined but should be considered in further studies. This section also suggests potential approaches to build on findings from this study in order to increase our understanding of the many variables that influence the range extension of marine species.

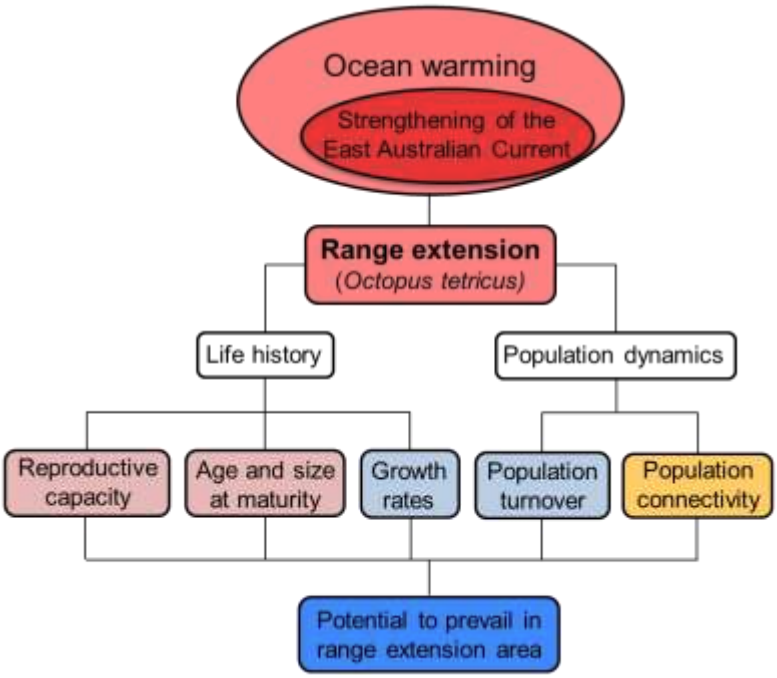


Figure 1.4 Schematic outline of the thesis "Life-history and population dynamics of the range extending *Octopus tetricus* (Gould, 1852) in south-eastern Australia". Chapters are represented by colour. Chapter 1, general introduction (red); Chapter 2, growth rates and population turnover (pale blue); Chapter 3, reproduction (pale red); Chapter 4, population genetics (yellow); Chapter 5, general discussion (bright blue)

# Chapter 2

## Body size, growth and life span: implications for the polewards range shift of *Octopus tetricus* in south-eastern Australia

This research is published as:

**Ramos JE**, Pecl GT, Moltschaniwskyj NA, Strugnell JM, León RI, Semmens JM (2014) Body size, growth and life span: implications for the polewards range shift of *Octopus tetricus* in south-eastern Australia. *PLoS ONE* 9, e103480. doi: 10.1371/journal.pone.0103480

**Abstract**

Several marine species are changing their patterns of geographic distribution in response to oceanic warming. However, the magnitude of such range shifts is highly variable, which is likely influenced by the life history characteristics of the range-shifting species. *Octopus tetricus*, a commercially important species, has undergone a recent polewards range shift in the coastal waters of south-eastern Australia, thought to be associated with the southerly extension of the warm East Australian Current. Population viability of *O. tetricus* at the range extension area may be affected as its life history characteristics are exposed to different environmental conditions. Growth rates, body size, and life span of *O. tetricus* were thus examined at the leading edge of the polewards range shift in Tasmanian waters (40°S and 147°E) throughout 2011. *Octopus tetricus* had fast growth rates, relatively small body size and short lifespan of approximately 11 months. Rapid population turnover may facilitate the size of the population to increase and establish in the new extended area of the range. Temperature, food availability and gender appear to influence growth rate. Individuals that hatched during cooler and more productive conditions, but grew during warming conditions, exhibited faster growth rates and reached smaller body sizes than individuals that hatched into warmer waters but grew during cooling conditions. This study suggests that fast growth, small body size and associated rapid population turnover may facilitate the range shift of *O. tetricus* into Tasmanian waters.

**Keywords:** Gloomy/Common Sydney octopus, stylet growth increments, ocean warming, East Australian Current, climate change.

## Introduction

The distribution and abundance of marine species depends on their functional traits and associated biotic factors, i.e. population genetic structure and gene flow (Holt 2003), physiological limits (Rosa & Seibel 2008; Calosi *et al.* 2010; Sunday *et al.* 2012), phenotypic plasticity (Engel *et al.* 2011), dispersal ability (Cowen & Sponaugle 2009; Travis *et al.* 2013), and intra and inter-specific interactions (Colautti *et al.* 2006; Blois *et al.* 2013). These functional traits and biotic factors are in turn modulated by abiotic factors such as temperature, oxygen and pH (Rosa & Seibel 2008; Calosi *et al.* 2013). Temperature is by far the easiest abiotic factor to record and therefore the most studied environmental variable. Moreover, all aspects of ectotherm behaviour and physiology are sensitive to environmental temperature (Pörtner & Farrell 2008), and species changes in distribution in response to climate change are thought to be largely driven by fluctuations in temperature (Poloczanska *et al.* 2013). However, there are substantial inter-specific differences in the magnitude of changes in distribution in response to such temperature variability (Sunday *et al.* 2012), and we have little knowledge about the processes responsible for the vast variation in species responses. Some studies have suggested that in response to ocean warming, marine species with fast growth rates, short lifespans, high genetic diversity, high dispersal capacity, e.g. with a planktonic larval stage or high migration potential, and that live near their upper thermal limit may be more able to change their distribution as they track their optimum thermal conditions (Parmesan & Yohe 2003; Pörtner & Farrell 2008; Sunday *et al.* 2012; Pinsky *et al.* 2013).

Long-term data sets appropriate to examine the response in life history parameters of long-lived species that may be undergoing climate-driven range shifts

are rarely available (Hoving *et al.* 2013). In contrast, ecologically and commercially important cephalopods (Clarke 1996) may facilitate the examination of such life history parameters as a function of their generally short lifespan (Mangold 1983a). The gloomy or common Sydney octopus, *Octopus tetricus*, is a merobenthic species with a planktonic paralarval stage of 2.2 mm ± 0.01 s.e. at hatching size (Ramos *et al*. unpubl. data) that is subjected to ocean currents. The duration of the paralarval stage before settlement is unknown for *O. tetricus* but it is assumed to be similar to that of closely related species (Guzik *et al.* 2005), i.e. 35–60 days for *O. vulgaris* reared under laboratory conditions (Villanueva 1995; Carrasco *et al.* 2006). *Octopus tetricus* reaches an approximate arm-span of 2 m (Norman & Reid 2000; Rowling *et al.* 2010). This species is commonly distributed in temperate waters of the east coast of mainland Australia, from southern Queensland to southern NSW as suggested by scientific surveys (Edgar 2000; Norman & Reid 2000). However, its distribution has extended polewards to south-eastern Australia, along the coasts of Victoria (see Villanueva & Norman 2008) after 2000 approximately, and eastern Tasmania in 2006 (as reported by fisheries data, i.e. Tasmanian Department of Primary Industries and Water 2009; and supported by citizen science monitoring using scientist-verified and geo-referenced photographs, i.e. Johnson *et al.* 2011; Range Extension Database and Mapping Project-REDMAP 2013). This polewards shift in distribution, like many others in the same area (Johnson *et al.* 2011; Last *et al.* 2011), is thought to be related to the southern extension of the warm East Australian Current (EAC) (Ridgway 2007; Hill *et al.* 2008) and is consistent with expected changes in distribution promoted by climate driven warming (Poloczanska *et al.* 2013). The EAC flows from the southern Coral Sea and reaches the south-east coast of mainland Australia (Ridgway & Dunn 2003). Over the past 60 years the EAC has extended

approximately 350 km further south, along the relatively cool east coast of Tasmania (Ridgway 2007; Hill *et al.* 2008). The strenghtening of the EAC has resulted in the southern Tasman Sea warming at a rate of three to four times the global average, with the ocean temperatures in the region projected to increase by 3°C by 2070 (Poloczanska *et al.* 2007).

Like other cephalopods that are key components of trophic webs (Clarke 1996), *O. tetricus* may play an important ecological role in transition of the energy flux from low to high trophic levels; for example, by competing with other octopus species for ecologically and commercially important prey species (Wolf & White 1997; Okei 1999; Harrington *et al.* 2006). Furthermore, *O. tetricus* is an important target of the octopus fishery in its historical distribution (Rowling *et al.* 2010) and now also in the leading edge of its range extension, contributing 14% of the octopus catch. Thus, *O. tetricus* provides a good opportunity to examine the influence of environmental variability on life history characteristics, in particular growth rates, body size and lifespan; and how such characteristics may influence its capacity to become established in the new sections of its range. The hypothesis of this study is that *O. tetricus* has fast growth rates and rapid population turnover, which may favour establishment of the population in the range extension area. Therefore, this study aims to examine the effect of environmental variables on the life history characteristics of *O. tetricus* at the southern edge of the recent range shift, in particular the size structure, growth rates and lifespan, and discuss how these characteristics may potentially influence the establishment of this species in Tasmanian waters.

## Material and methods

*Collection of wild caught specimens*

Octopuses were collected by fishers using black plastic shelter pots, 0.3-m long × 0.1-m high × 0.1-m wide, laid on the seafloor at a depth of 35–46 m off the east coast of Flinders Island, north-eastern Tasmania (approximately 40°S and 147°E; Fig. 2.1) during January (*n* = 47), February (*n* = 78), April (*n* = 93), May (*n* = 92), July (*n* = 45), September (*n* = 76) and December (*n* = 96) 2011 on board of the commercial *FV Farquharson*.

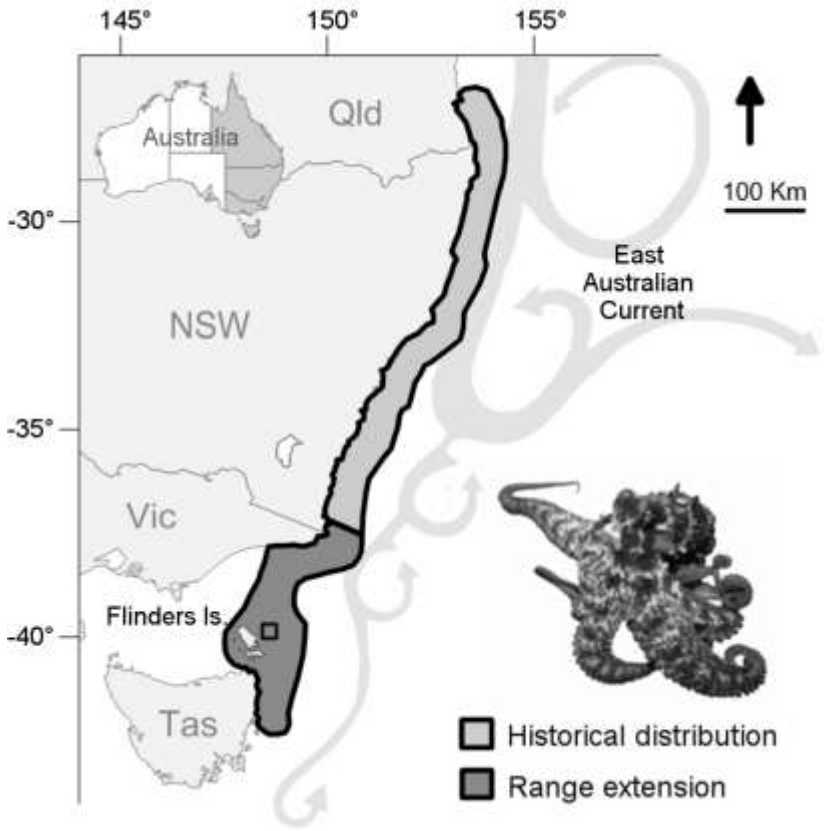


Figure 2.1 Collection area of *Octopus tetricus* off north-eastern Flinders Island at north-eastern Tasmania, Australia, during 2011. The collection area is indicated with the box. Qld, Queensland; NSW, New South Wales; Vic, Victoria; Tas, Tasmania. Photo of *O. tetricus* by R. Stuart-Smith

The whole animals were frozen on board at -20°C, except specimens collected during February and May 2011 which were preserved on board in 80% ethanol. Individuals were dissected in the laboratory and eviscerated total wet weight (TW) and mantle weight (MW) (g) were recorded. Mantle weight was preferred over TW because missing and incomplete arms from many individuals provided an underestimate of TW. However, TW was recorded to facilitate comparison with previous studies. Measurements and weights were recorded to the nearest 0.1 cm and 0.01 g respectively.

To correct weights of samples frozen at –20°C or preserved at 80% ethanol, sections of mantle tissue of 1-cm width × 2-cm length of different wild caught individuals were weighed fresh and frozen at –20°C ($n$ = 100) or preserved at 80% ethanol ($n$ = 86). Weight was recorded again after the same period that had passed between collection of wild caught specimens and weighing in the laboratory.

Sex and maturity (immature, mature and spent) were determined based on the macroscopic characteristics of the gonads. The maturity scale was modified from previous studies (Mangold 1983b; Dia 1988; see Supporting information, Table S2.1).

*Age estimation*

Stylets, the vestigial shells of octopods, have recently been used with success to estimate age and growth rates (Doubleday *et al.* 2006; Leporati *et al.* 2008a, 2008b; Barratt & Allcock 2010; Hermosilla *et al.* 2010; Herwig *et al.* 2012). Stylets were removed from the mantle of fresh specimens, specimens that were frozen at –20°C, and specimens that were preserved at 80% ethanol; stylets were then stored in 70% ethanol. Stylets of all specimens ($n$ = 527) were cut, embedded, ground, and

polished following (Barratt & Allcock 2010) with slight modifications: Two to five pictures, depending on the diameter of the stylet's section, were sequentially taken from the nucleus to the edge of the stylet's section. Pictures were taken at either ×100, ×200 or ×400 magnification (Fig. 2.2) using the software Leica Application Suite (LAS) v. 3.6.0 (Leica Microsystems, Switzerland) with a transmitted-light microscope Leica DM LB2 connected to a digital camera Leica DFC420. Pictures were sequentially stitched together and daily increments identified following Doubleday *et al.* (2006). Two non-consecutive increment counts were made by one reader using a key counter software (KeyCounter v. 1.1.0), and a third count was carried out by a second reader. Stylet sections were discarded ($n$ = 313) if growth increments were not clear along the section, if more than 10% of the section was unable to be counted, and if the three counts differed by more than 10%. The mean of the three counts of the growth increments of each stylet's section was considered as the total number of growth increments. To estimate the age of each individual the daily periodicity of growth increments was assumed as it has been validated or assumed for holobenthic (*O. pallidus*: Doubleday *et al.* 2006) and merobenthic octopods like *O. tetricus* (i.e. *O. vulgaris*: Barratt & Allcock 2010; Hermosilla *et al.* 2010; *Eledone cirrhosa*: Barratt & Allcock 2010; *O. cyanea*: Herwig *et al*. 2012; *O.* cf. *tetricus*, Leporati & Hart 2014). Of these species, *O. vulgaris* and *O.* cf. *tetricus* are genetically closely related to *O. tetricus* (Guzik *et al*. 2005; Amor *et al*. 2014). The hatch date of each individual was estimated by subtracting the estimated age from the date of capture of the individual (females: $n$ = 103, 7–193 g mantle weight; males: $n$ = 111, 8–161 g mantle weight).

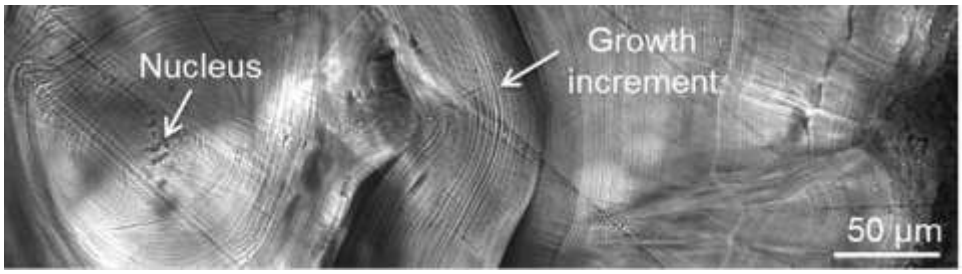


Figure 2.2 Stylet of *Octopus tetricus*. Microstructure of a stylet's transverse section where growth increments are observed

*Oceanographic data*

Monthly SST and chlorophyll-*a* concentration (Chl-*a*) data for the area of collection were obtained from the MODISA satellite imagery at a 4-km scale (http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/Monthly/4km/, accessed 11 November 2012). Oceanographic data were processed using MATLAB v. 7.2 (R2006a) (The MathWorks, Natick, MA). *Octopus tetricus* was collected at shallow depths (35–46 m) where wind-driven mixing is high and tidal currents are strong (Sandery & Kämpf 2007); therefore SST was considered a valid temperature estimate of the habitats occupied by *O. tetricus*. Chlorophyll-*a* concentration is an estimator of primary productivity, often with strong links to biomass of higher trophic levels (Ware & Thomson 2005; Otero *et al*. 2008), and was therefore considered an indirect estimator of food availability for *O. tetricus*.

*Data analysis*

Paired sample t-tests were used to assess significant differences between fresh samples and those frozen at –20°C, and between fresh samples and those preserved in 80% ethanol. Model II linear regressions were conducted when necessary to adjust weights of samples frozen at –20°C or preserved in 80% ethanol

so they were comparable to fresh weights. All data were Box-Cox transformed when necessary using the "car" package in R v. 3.0.1 (Fox & Weisberg 2011; R Core Team 2013). Normality was determined visually and using the Shapiro-Wilk's test. Homogeneity of variances was evaluated by visual inspection of residual plots.

Hatch month of each individual was back-calculated, by subtracting an individuals estimated age (days) from its date of capture. Hatch months were grouped into a 'warm season' including December to May (17.6°C ± 0.38 s.e. and 0.70 mg Chl-*a* $m^{-3}$ ± 0.04 s.e., $n$ = 12) and a 'cool season' of June to November (13.2°C ± 0.30 s.e. and 0.90 mg Chl-*a* $m^{-3}$ ± 0.07 s.e., $n$ = 12) (following Moreno *et al.* 2012). Maximum life span was considered a proxy of population turnover.

The Gompertz, exponential, power and linear growth models were generated for mantle weight of females and males pooled by season of hatching. The 3-parameter Gompertz growth model had the smallest Akaike Information Criterion (AIC), its Akaike weight (wAIC) was closest to 1 (Akaike 1974; Wagenmakers & Farrell 2004) using the package "qpcR" in R v. 3.0.1 (R Core Team 2013; Spiess 2013), and thus was identified as the model that best fitted the size (MW) at age data (Supporting information, Table S2.2). The Gompertz growth model was constructed using the non-linear weighted least square method following (Arkhipkin & Roa-Ureta 2005):

$$m(a) = m_{\infty} e^{-\gamma \exp(-g_1 a)}$$

Where

$$\gamma = \frac{\ln m_2 - \ln m_1}{1 - e^{-g_1 a_2}}, \qquad m_{\infty} = m_0 e^{\gamma},$$

$$\mu = m_{\infty} e^{-1}, \qquad SE_{\mu} = \sqrt{SE_{m_{\infty}}{}^2 (e^{-1})^2},$$

Where $m$ is mantle weight (g); $a$ is age (days); $m_\infty$ is the asymptote parameter in $m(a)$ (g); $\gamma$ is the shape parameter in $m(a)$; $g_1$ is the rate coefficient parameter in $m(a)$ ($day^{-1}$); $m_1$ and $m_2$ are location parameters in $m(a)$ (g), or predicted mantle weight at minimum or maximum observed age; $a_2$ is the maximum observed age; $\mu$ is the inflection point parameter in $m(a)$ (g) and SE is the standard error. The three parameters to estimate are $m_\infty$, $\gamma$ and $g_1$. The 95% confidence intervals for the coefficients of the Gompertz growth model were estimated by bootstrapping using the package "car" in R v. 3.0.1 (Fox & Weisberg 2011; R Core Team 2013). The F-statistics was calculated through an analysis of residual sum of squares (ARSS) to compare Gompertz growth models between genders and among warm and cool hatching seasons (Chen *et al.* 1992). The instantaneous relative rate of growth ($G$) for the Gompertz model was estimated following (Arkhipkin & Roa-Ureta 2005):

$$G = \hat{\gamma}\hat{g}_1 e^{-g_1 a}$$

A two-way ANOVA was used to compare differences in MW of mature females, and mature and spent males, as well as to compare differences in age of mature and spent females and mature and spent males among warm and cool seasons of hatching. All statistics and models were carried out using R v. 3.0.1 (R Core Team 2013).

## Results

*Body size and life span*

A total of 527 *Octopus tetricus* (250 females and 277 males) were collected during 2011, approximately 40% of which were smaller than 40 g in MW. Mantle

weight distribution was not significantly different between females (5–209 g) and males (3–189 g, Fig. 2.3) (ANOVA, $F_{(1,505)} = 0.338$, $P > 0.56$); with TW ranging between 60–2260 g for females and 50–2100 g for males. Age of females was not significantly different from age of males (ANOVA, $F_{(1,212)} = 0.039$, $P = 0.84$); females were estimated to be 85–308 days ($n = 103$) of age and males 88–313 days ($n = 111$, Fig. 2.3). Maximum life span was 11 months.

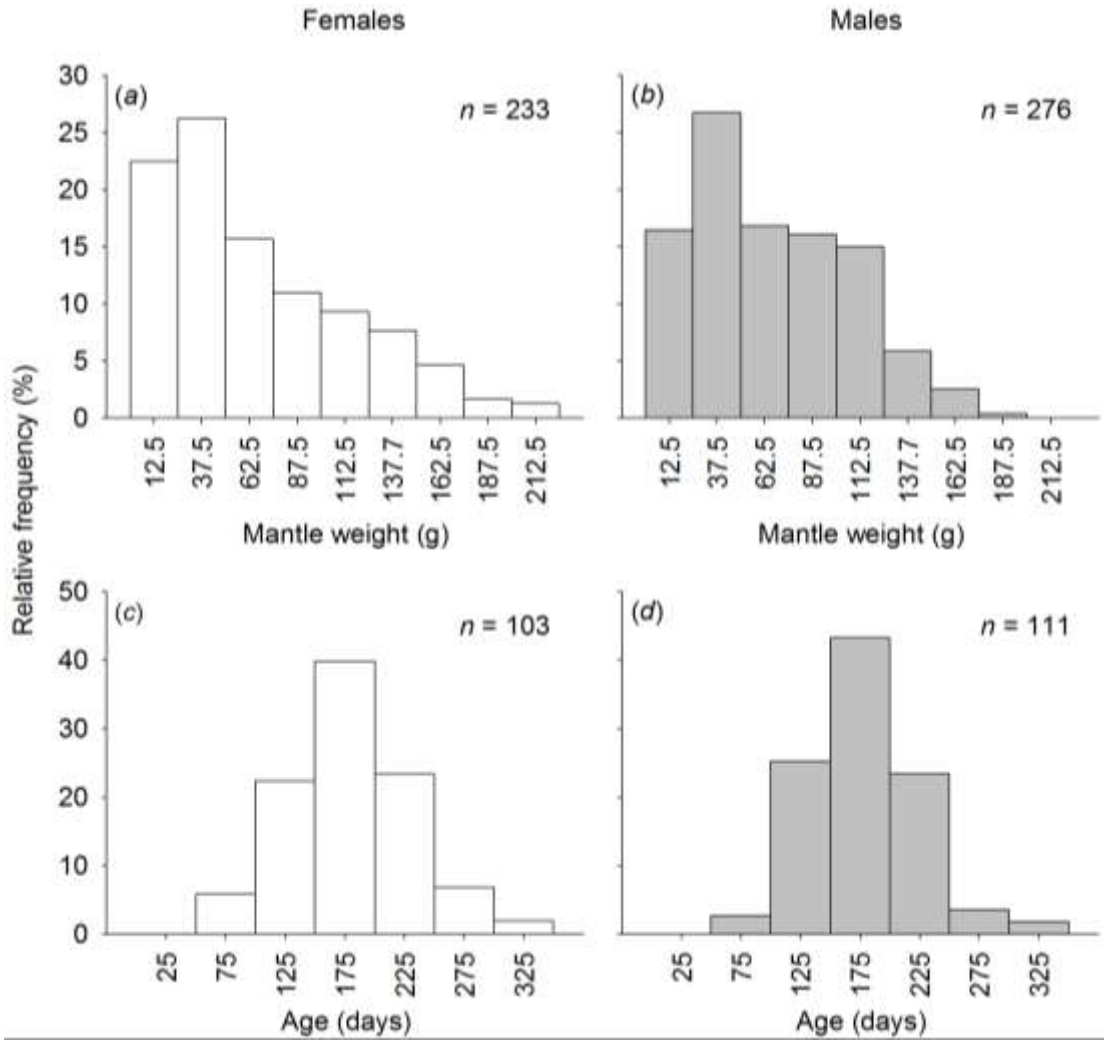


Figure 2.3 Relative frequency (%) of female and male *Octopus tetricus* at (*a–b*) mantle weight (g) and (*c–d*) age (days), respectively at the range extension off north-eastern Tasmania, Australia during 2011

*Growth rates, body size and life span at hatch seasons*

Individuals collected in 2011 hatched throughout 2010 and 2011. Greatest numbers of these animals hatched in 2010 when SST was at coolest and Chl-*a* concentration highest (Fig. 2.4). A second hatching peak was observed in January 2011 when SST was increasing and Chl-*a* concentration was decreasing. The estimated average instantaneous relative growth rate ($\hat{G}$) of all *O. tetricus* in north-eastern Tasmania was 0.014 $\hat{G}$ day$^{-1}$ ± 0.0006 s.e., $n$ = 214 (Table 2.1). The ARSS indicated that growth models differed between hatching seasons ($F_{(3,211)}$ = 7.03, $P$ < 0.0001; Fig. 2.5). For instance, instantaneous relative growth rate of cool hatched animals was significantly faster than the instantaneous relative growth rate of warm hatched animals (Table 2.1). Growth models differed only between females and males that hatched in the warm season ($F_{(3,77)}$ = 2.79, $P$ < 0.0001).

Approximately 14% of captured females and 44% of captured males were mature or spent. Maximum MW of mature females was significantly different between hatching seasons (ANOVA, $F_{(1,10)}$ = 13.2, $P$ = 0.005), with females that hatched during the warm season heavier (144.89 g ± 8.56 s.e., $n$ = 5) than females that hatched in the cool season (94.92 g ± 9.83 s.e., $n$ = 7). Similarly, mature and spent males that hatched in the warm season were heavier (120.28 g ± 7.24 s.e., $n$ = 19) than males that hatched in the cool season (92.20 g ± 7.09 s.e., $n$ = 22; ANOVA, $F_{(1,39)}$ = 7.61, $P$ = 0.009). Considering only mature and spent females, individuals that hatched in the warm season were significantly older (271 days ± 11.72 s.e., $n$ = 6) than females that hatched in the cool season (194.75 days ± 13.26 s.e., $n$ = 8; ANOVA, $F_{(1,12)}$ = 17.13, $P$ = 0.001). In contrast, age of mature and spent males that hatched in the warm season (196.32 days ± 7.15 s.e., $n$ = 19) did not differ

significantly from the age of males that hatched in the cool season (218.32 days ± 9.49 s.e., $n$ = 22; ANOVA, $F_{(1,39)}$ = 3.26, $P$ = 0.08).

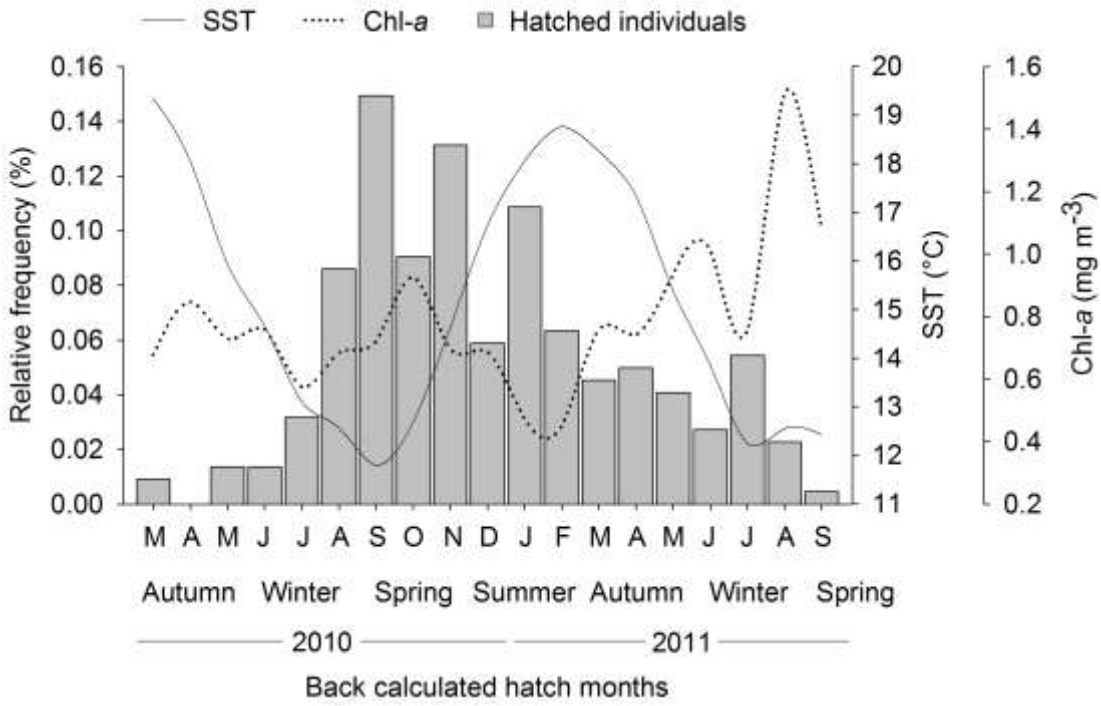


Figure 2.4 Monthly relative frequency (%) of hatched *Octopus tetricus* ($n$ = 214) from north-eastern Tasmania, Australia during 2010 and 2011

Table 2.1 Parameter estimates for the 3-parameter Gompertz growth model fitted to mantle weight at age, and instantaneous relative growth rate for backed calculated hatched *Octopus tetricus* from north-eastern Tasmania, Australia collected during 2011

| | n | Age (days) | $\hat{\mu}$ (g) | $\hat{\gamma}$ | $\hat{g}_1$ (day$^{-1}$) | $\hat{G}$ (day$^{-1}$) |
|---|---|---|---|---|---|---|
| By hatch season | | | | | | |
| w | 80 | 91–301 | 57.90 (4.93) | 10.15 (2.50) | 0.016 (0.0023) | 0.012 (0.001) |
| c | 134 | 85–313 | 61.06 (2.88) | 12.20 (1.52) | 0.015 (0.0009) | 0.016 (0.0009) |
| By gender | | | | | | |
| f | 103 | 85–308 | 88.77 (13.91) | 7.05 (0.76) | 0.009 (0.001) | 0.013 (0.0006) |
| m | 111 | 88–313 | 54.67 (1.09) | 13.77 (1.19) | 0.017 (0.0007) | 0.014 (0.001) |
| All | 214 | 85–313 | 63.11 (3.54) | 9.81 (1.03) | 0.0137 (0.0009) | 0.014 (0.0006) |

$\hat{\mu}$ = inflection point parameter in mantle weight (age) (g); $\hat{\gamma}$ = shape parameter in mantle weight (age) (g); $\hat{g}_1$ = rate coefficient parameter in mantle weight (age) (day$^{-1}$); $\hat{G}$ = instantaneous relative growth rate (day$^{-1}$); c = cool; w = warm; f = females; m = males. Asymptotic standard errors indicated in parenthesis. Significance for estimated parameters $P < 0.05$

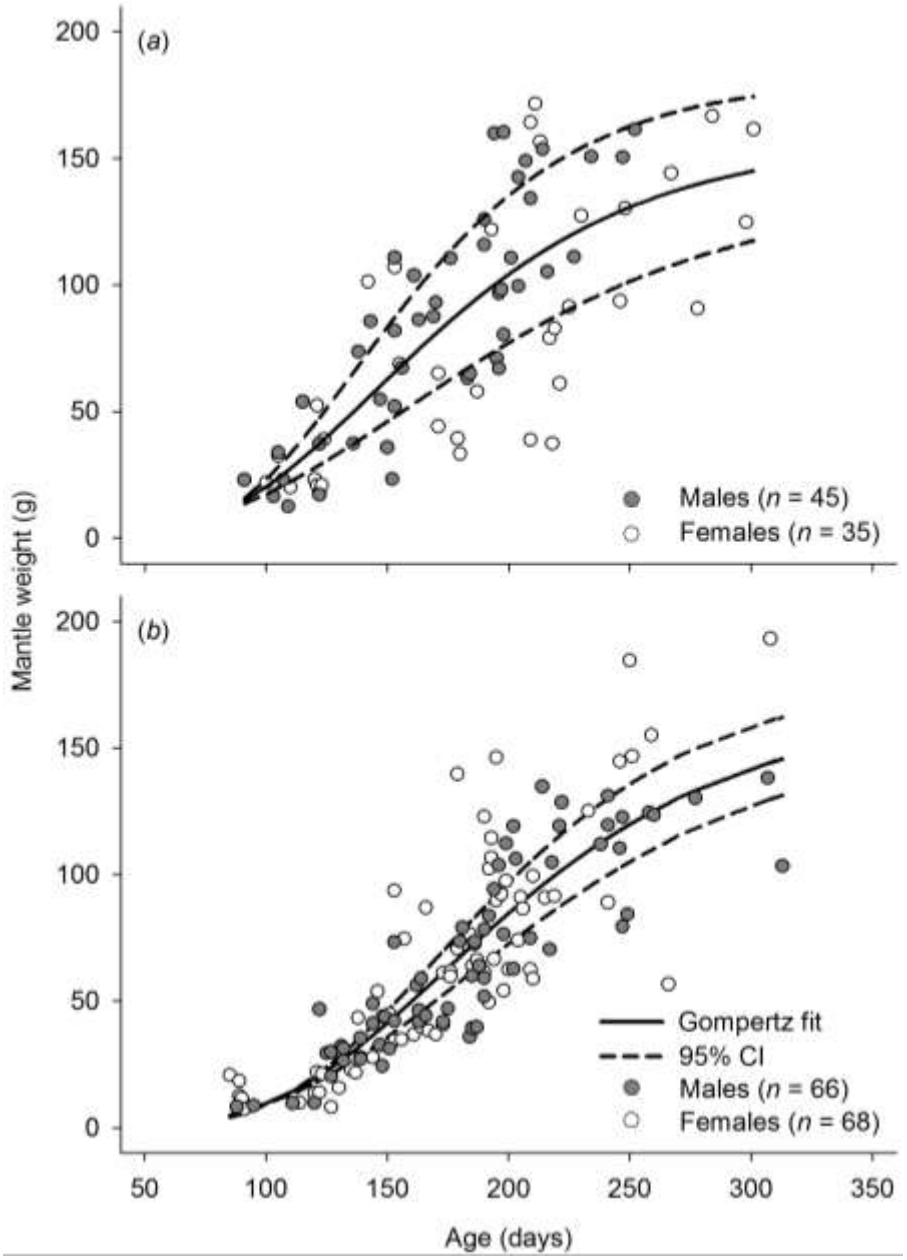


Figure 2.5 Growth of *Octopus tetricus.* Mantle weight (g) and age (days) data, and fitted 3-parameter Gompertz growth model for individuals that hatched in (*a*) warm and (*b*) cool seasons at north-eastern Tasmania, Australia. Individuals were collected during 2011 and hatch seasons were back-calculated from growth increments in stylets. CI = Confidence interval

**Discussion**

This study demonstrates that *Octopus tetricus* has a fast growth rate, small body size and a short lifespan of approximately 11 months at the leading edge of its polewards range extension. These characteristics correspond to an *r*-selected life history strategy, which would facilitate the apparent rapid population expansion of this species and assist the 'invasion' into new environments (McMahon 2002; Amundsen *et al.* 2012). Fast growth rates and short lifespan, combined with successful reproduction, i.e. mating, high fecundity and production of viable embryos (Ramos *et al*. 2015), may underpin a capacity for *O. tetricus* to quickly increase the size of the emerging population in the zone of the range extension. Additionally, such a short lifespan and associated high population turnover may give *O. tetricus*, most likely an efficient generalist predator like most other octopus species (Anderson *et al.* 2008; Mather *et al*. 2012), a competitive advantage in the short term (see Fulton 2011) over the longer-lived species already found within the new range area.

Most individuals collected in the relatively cooler Tasmanian waters during 2011 (annual average 15.3°C ± 2.4 s.d.) were quite small (<0.4 kg TW) with the maximum of 2.3 kg TW measured, compared with larger individuals (>3 kg TW, S. Montgomery pers. comm.) reported from the warmer NSW waters (annual average 20.3°C ± 2 s.d.). Life history characteristics, i.e. growth rates, body size and life span, may differ over the distribution of a species, and may even diverge at the extension of the species distribution (Amundsen *et al.* 2012) possibly a function of reduced genetic diversity (Arenas *et al.* 2012), or altered as an adjustment to the new physical environment (Pörtner & Farrell 2008), or to different community interactions (Shea & Chesson 2002). For example, body size may be smaller in the

region of range extension even though life-history theory predicts body size should be larger in cooler waters. Alternatively, the use of shelter pots may have led to aggregation of mature females or limited the body size of *O. tetricus* collected in Tasmanian waters. In contrast, the use of trawl nets in NSW would not lead to aggregation of mature females or limit the body size of captured octopuses. However, additional evidence suggests that the age at sexual maturity (206 days ± 26 s.d., $n$ = 214; Ramos *et al*. 2015) and time for egg laying and embryo development in Tasmania (~60 days; unpubl. data) fits within the estimated life span (~11 months) of *O. tetricus*. Therefore, maximum body size and life span do not seem to have been underestimated in the range extension area. This is further supported by the similar lifespan of other merobenthic octopods, e.g. *O. cyanea* (11 months; Herwig *et al.* 2012), *O. vulgaris* (12–15 months; Domain *et al.* 2000; Katsanevakis & Verriopoulos 2006; Canali *et al.* 2011), or *O. bimaculoides* (14 months; Forsythe & Hanlon 1988).

A short lifespan can facilitate rapid population turnover. Selection acts on biological traits of every generation (Lee 2002); thus, favoured genotypes are likely to be selected more often in species with shorter generation times (Berteaux *et al.* 2004; Hoffmann & Willi 2008) due to greater probability of occurrence of mutations or formation of new gene complexes (Parmesan 2006). In this sense, it is possible that the combined effects of small body size, short life span, and likely rapid adaptation to environmental changes and biotic pressures may allow exploitation of niches, which may facilitate the establishment of *O. tetricus* in the leading edge of the range shift into Tasmanian waters.

The 3-parameter Gompertz growth model was an appropriate fit for size at age of *O. tetricus*. This model has adequately described non-linear relationships for

growth estimations for other cephalopods taxa, e.g. squids (Arkhipkin & Roa-Ureta 2005; Schwarz & Alvarez-Perez 2010), and is simpler than other models, i.e. the 4-parameter Schnute growth model (Arkhipkin & Roa-Ureta 2005). To my knowledge, this is the first study that suggests the Gompertz model as the best fit for growth of an octopod. Therefore, it is not possible to compare with growth models of other octopods. In contrast, the instantaneous growth rate estimated in this study is comparable only to those estimated during the exponential growth of octopods using the equation ($G = (\ln W_2 - \ln W_1)/(t_2 - t_1)$) (Forsythe & Van Heukelem 1987; Arkhipkin & Roa-Ureta 2005). *Octopus tetricus* shows similar growth rates compared to wild caught octopods in their historical distribution, e.g. 0.011 $G$ day$^{-1}$ ± 0.003 s.e., $n$ = 628 for *O. vulgaris* (Domain *et al.* 2000), and octopods in captivity, e.g. 0.014 $G$ day$^{-1}$ ± 0.0004 s.e., $n$ = 18 for *O. pallidus* (Semmens *et al.* 2011), 0.018 $G$ day$^{-1}$ ± 0.002 s.e. for *O. maya*, $n$ ~40 (from Rosas *et al.* 2008), and 0.036 $G$ day$^{-1}$ ± 0.005 s.e., $n$ = 84 for *O. bimaculoides* (Forsythe & Hanlon 1988). Fast growth rates, short life span and associated rapid population turnover may facilitate the establishment of *O. tetricus* at the range extension in Tasmanian waters.

*Influence of environmental factors on growth rates*

The estimated frequency of hatched individuals may have been masked by gaps in the collection of specimens during some months, in addition to natural processes such as predation, natural mortality, etc. that were not accounted in this study. With this in mind, these results show that *O. tetricus* hatched throughout the year, with greater number of hatched individuals during the cool and highly productive season. Individuals that hatched in cool and under higher Chl-*a* concentration experienced warming conditions later in their life. Those individuals

grew faster and achieved smaller body sizes than individuals that hatched in warm conditions, under low Chl-*a* concentration, and grew during cooling conditions (Fig. 2.6). Thus, the initial greater peaks of Chl-*a* (and inferred greater availability of food), combined with increasing temperatures after hatching may be related to the faster growth rate of individuals hatched in cool conditions. Similarly, reproductive events of *O. vulgaris* seem to be synchronized with local events of high productivity (Oosthuizen & Smale 2003; Otero *et al.* 2007; Lourenço *et al.* 2012) that eventually may benefit hatchlings with greater availability of resources (Otero *et al.* 2008). Likewise, squids have experienced faster growth rates in cool waters and this has been attributed to increased productivity or availability of food (*Todarodes angolensis*, Villanueva (1992); *Loliolus noctiluca*, Jackson & Moltschaniwskyj (2001); *Loligo opalescens*, Jackson & Domeier (2003)).

Size at age variability was observed as aged increased. Individual growth variability has also been noted in other studies (Arkhipkin & Roa-Ureta 2005; Leporati *et al.* 2007; Canali *et al.* 2011; Herwig *et al.* 2012). Such variability in response to environmental factors, particularly to temperature, has been extensively studied in squids (Forsythe & Van Heukelem 1987). Yet, the relationship of growth in octopods and environmental variability is far from understood (Semmens *et al.* 2004) and other biological factors such as gender, reproduction, genetics and physiological traits must be considered. For instance, differential growth of females and males has been observed during the slower phase of growth with the start of sexual maturity (Forsythe & Van Heukelem 1987), which may explain the different growth rates observed between females and males that hatched in the warm season. This suggests that SST, availability of food, and probably other environmental and biotic factors influenced growth rates at different levels. Therefore, growth must be

studied considering the interaction of environmental and biotic factors, in order to disentangling their individual effects.

This study has provided biological information on age and growth of *O. tetricus* at the leading edge of a recent and rapid range shift. The synchrony of hatching events with environmental conditions, such as availability of higher food concentration and warmer temperatures, appears to have a large influence on growth rates, body size and life span of this octopus. The estimated life span of 11 months may allow *O. tetricus* to cope with environmental variability and possibly facilitate exploitation of available niches. Additional studies on population linkages, reproductive biology (e.g. Ramos *et al*. 2015), trophic ecology, thermal physiology, and dispersal or migration capacity are essential to develop a more complete understanding of the capacity of a species to alter its range and comprehend the biological and ecological mechanisms that underpin range extensions.

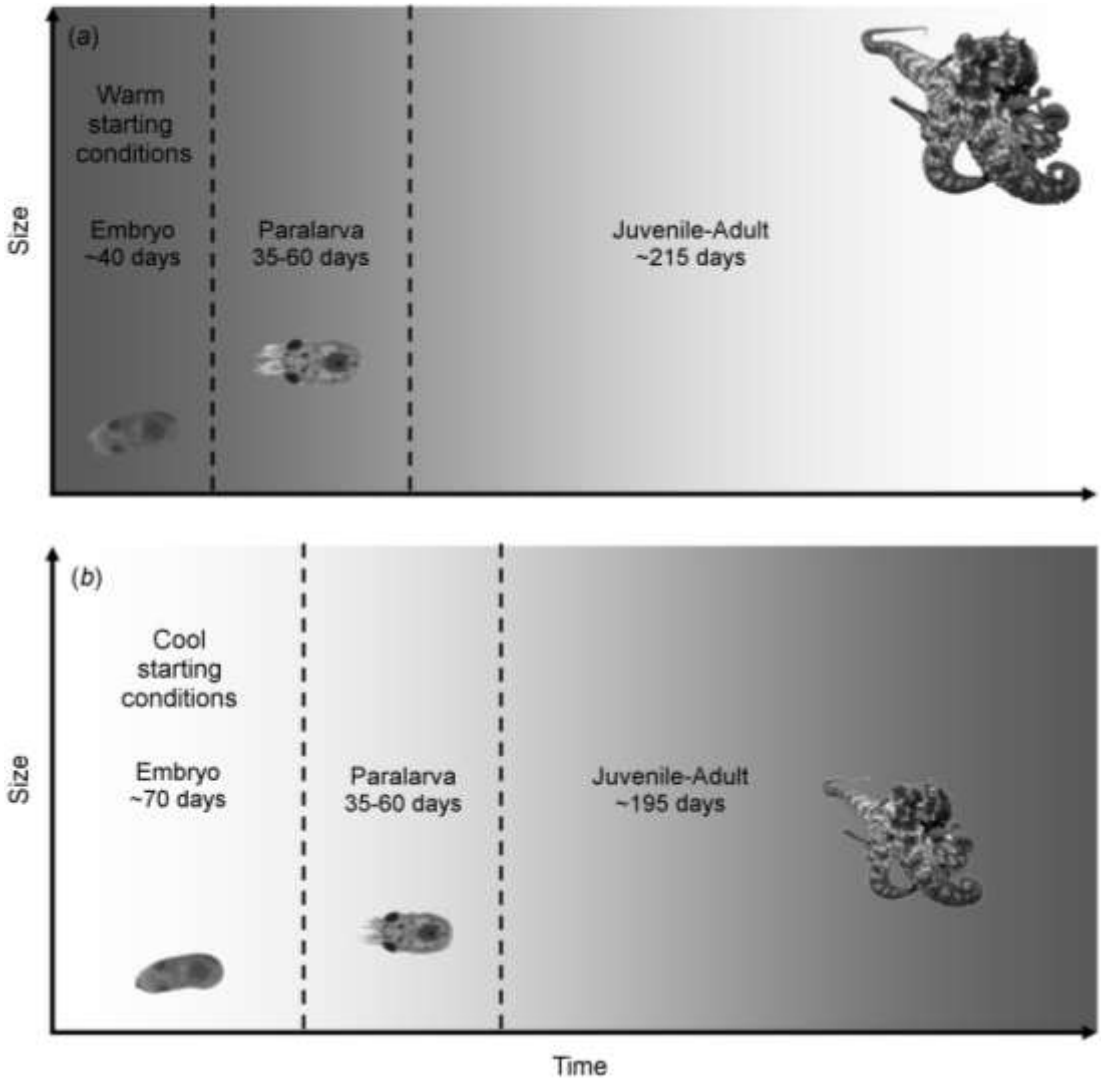


Figure 2.6 Life cycle of *Octopus tetricus*. (*a*) Octopuses that hatch in warm temperatures have a shorter embryonic phase and likely have faster growth during the exponential phase (embryo and paralarva). Decreasing temperatures during the juvenile and adult phases lead to slower growth resulting in longer life span and larger body size. Note the gradient of temperature from warm (dark grey) to cool (light grey). (*b*) Octopuses that hatch in cool temperatures have a longer embryonic phase and slower growth during the exponential phase (embryo and paralarva). Increasing temperatures during the juvenile and adult phases lead to faster growth resulting in shorter life span and smaller body size. Note the gradient of temperature from cool (light grey) to warm (dark grey). Photo of adult *O. tetricus* by Rick Stuart-Smith

*Acknowledgments*

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# Chapter 3

## Reproductive capacity of a marine species (*Octopus tetricus*) within a recent range extension area

This research is published as:

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**Abstract**

To persist in the face of environmental change, species must adjust to the new conditions or change their geographical distribution, e.g. by range extension. Success for individuals within a zone of range extension requires the new environment to support their capacity to produce viable gametes and survival of the offspring. Reproductive characteristics of the polewards range-shifting *Octopus tetricus* were examined within the new range off north-eastern Tasmania, Australia, to assess whether it is likely to successfully establish in this extended area of its range. Approximately 44% of captured males and 14% of captured females were mature. Mature females with developing eggs were found throughout the year. Greater numbers of mature females were observed during the austral summer and spring, whereas mature males were observed all year round. Fecundity was high and developing embryos appeared to be viable. Our results suggest that *O. tetricus* is successfully reproducing beyond its historical range, the reproductive cycle is timed to favourable environmental conditions, and the population has the potential to be self-sustainable. The reproductive capacity of *O. tetricus* may thus facilitate the establishment and prevalence of the population into new environments beyond the known historical distribution.

**Keywords:** East Australian Current, fecundity, Ocean warming, population dynamics, population establishment, range shift.

## Introduction

The heat content of the world's oceans has increased $24 \times 10^{22}$ J, representing a volume mean warming of 0.09°C in the 0–2000 m layer, since 1955 (Levitus *et al.* 2012). Worldwide, there are 24 regions or 'hotspots' where ocean surface temperatures have changed most rapidly over the past 50 years, and are likely to continue to change rapidly in the future (Hobday & Pecl 2014). One of those 'hotspots' is located in the western Tasman Sea off the south-east coast of Australia (Hobday & Pecl 2014). The rapid warming of the south-east coast of Australia is in part caused by the extension of the East Australian Current, which is the major western boundary current of the South Pacific subtropical gyre that flows from the southern Coral Sea and reaches the south-east coast of mainland Australia (Ridgway & Dunn 2003). However, over the past 60 years the East Australian Current has extended ~350 km south, penetrating further along the east coast of Tasmania (Ridgway 2007; Hill *et al.* 2008). As a result the rate of warming off south-east Australia is up to four times faster than the global average, with the ocean temperatures in the region projected to increase by 3°C by 2070 (Poloczanska *et al.* 2007). In response to ocean warming many marine species, mostly ectotherms (e.g. *Centrostephanus rodgersii*, Ling *et al.* 2009), are shifting their distribution to occupy their preferred thermal environment (Parmesan & Yohe 2003; Sunday *et al.* 2012; Pinsky *et al.* 2013). Accordingly, the range shift of more than 70 marine species along the east coast of Tasmania appear to be associated with the extension of the East Australian Current (Ling *et al.* 2009; Pitt *et al.* 2010; Last *et al.* 2011).

The common Sydney octopus, *Octopus tetricus*, is one of the species documented to be shifting polewards in eastern Australia (Villanueva & Norman 2008; Johnson *et al.* 2011; Amor *et al.* 2014; Ramos *et al.* 2014; Robinson *et al.*

2015). The historical distribution of *O. tetricus* in Australia is from the warm waters of southern Queensland to southern NSW (Edgar 2000; Norman & Reid 2000). However, its distribution has extended in recent years to include Victoria (Villanueva & Norman 2008), as confirmed by systematic marine life census (Edgar & Stuart-Smith 2014). Since 2006, *O. tetricus* has also been detected further south in the warming but still comparatively cool north-eastern Tamania (Fig. 2.1), as suggested for the first time by octopus fishery records (Tasmanian Department of Primary Industries and Water 2009; C. Hardy, pers. comm.). The range extension of *O. tetricus* into Tasmanian waters is also supported by citizen science submitted data with scientist-verified and geo-referenced photographs (REDMAP), see http://www.redmap.org.au, accessed 4 September 2013), systematic marine life census (Edgar & Stuart-Smith 2014) and scientific studies (Johnson *et al.* 2011; Amor *et al.* 2014; Ramos *et al.* 2014; Robinson *et al.* 2015). Based on the duration of the planktonic paralarval phase of the closely related *O. vulgaris* (Guzik *et al.* 2005; Amor *et al.* 2014), i.e. 35–60 days under laboratory conditions (Villanueva 1995; Carrasco *et al.* 2006), *O. tetricus* paralarvae could be dispersed for up to 60 days. The range extension of *O. tetricus* may thus be facilitated by the East Australian Current, which is likely to disperse the planktonic paralarvae of *O. tetricus* from the historical range into Tasmanian waters.

Successful establishment of populations of *O. tetricus* south of their historical range would require environmental conditions that support growth of individuals to maturity, including the capacity to produce viable gametes and survival of the subsequent offspring. Over its historical range *O. tetricus* is exposed to a gradient of sea surface temperatures (SST): 18–22°C during the austral winter and summer (annual average 20.2°C ± 0.2 s.e. at 32°31’15”S, 152°28’45”E). In the range

extension areas SSTs are 13–18°C during the austral winter and summer (annual average 15.2°C ± 0.2 s.e. at 39°33'45"S, 148°13'45"E). The narrow overlap of SST between the historical distribution and range-extension areas may have negative consequences for the reproductive capacity of *O. tetricus*, and on its capacity to establish and prevail in the range-extension area. *Octopus* cf. *tetricus,* a temperate Western Australia sister species of *O. tetricus* (Guzik *et al*. 2005; Amor *et al*. 2014), is found at similar latitudes to *O. tetricus* in its historical distribution on the east coast. Male *O.* cf. *tetricus* reach maturity at 941 g total weight and 243 days, and females reach maturity at 1794 g total weight and 379 days (Leporati *et al.* 2015). Females lay eggs in hundreds of strings of 10–12 cm long each, with a mean of 125 eggs $cm^{-1}$ and an estimated total of 150,000 eggs per string, with potential fecundity estimated in 705,000 eggs. Length and width of the eggs are 2.4 mm and 0.9 mm respectively, and paralarvae are 2.5 mm total length when they hatch 22–36 days after eggs deposition (Joll 1976). Cephalopods have flexible life histories largely due to their rapid response in growth to changes in temperature, with slower growth rates at lower temperatures (Forsythe & Van Heukelem 1987; Forsythe 2004). Assuming that minimum temperature thresholds for growth and reproduction are met in the range extension area, it is expected that *O. tetricus* would mature late and at a large size, probably resulting in great potential fecundity in the cool waters of the range-extension area. However, individual metabolic rates, and therefore reproduction, could be negatively affected if the new sections of the distribution do not provide favourable environmental conditions and resources (Pörtner & Farrell 2008; Kearney & Porter 2009; Calosi *et al.* 2013).

The reproductive biology of *O. tetricus* has not been studied in any part of its geographic distribution along the east coast of Australia despite the recent range

extension that this species of commercial interest is undertaking (Rowling *et al.* 2010). Therefore, we examined the reproductive biology of *O. tetricus* in north-eastern Tasmania to assess whether it has the potential to reproduce in the range-extension area. In particular, this study describes the reproductive condition of *O. tetricus*, size and age at maturity, fecundity, offspring viability, temporal pattern of reproductive events, and temporal changes in reproductive characteristics. Descriptions of reproductive traits during summer and winter months in the range-extension area will provide information about the influence of SST on these traits. Addressing these aims will help generate a description of the reproductive dynamics of *O. tetricus* within the range-extension area, and how they may relate to the potential of this range-shifting species to establish populations in new areas.

## Material and methods

### *Collection and processing of specimens*

In total, 527 specimens were collected off the east coast of Flinders Island off north-eastern Tasmania (approximately 40°S, 148°E; Fig. 2.1) as per Chapter 2. Dorsal mantle length was recorded and whole animals were frozen on board at –20°C, except individuals collected during February and May 2011 which were immediately preserved in 80% ethanol. Individuals were later dissected in the laboratory; eviscerated total weight (weight without digestive or reproductive organs) and mantle weight were recorded. Mantle weight was preferred over eviscerated total weight because missing and incomplete arms from many individuals provided an underestimate of eviscerated total weight. However, eviscerated total weight was recorded to facilitate comparison with previous studies. All animals were sexed and

included 250 females and 277 males. Reproductive organs were removed from the visceral mass and weighed individually. Female reproductive weight was defined as the combined weight of ovary, oviducal glands and oviducts. Male reproductive weight was defined as the combined weight of testis, Needham's sac and penis. Measurements and weights were recorded to the nearest 0.1 cm and 0.01 g. Measurements and weights of gonads and muscle frozen at –20°C or preserved at 80% ethanol were processed as per Chapter 2 so they were comparable to fresh weights and measurements.

*Age estimation and back calculated hatch month*

Stylets processing, and age and hatch date were estimated as per Chapter 2.

*Sex, maturity, reproductive-somatic condition*

A maturity stage of either (I) Immature, (II) Mature, or (III) Spent was determined for all individuals (see Supporting information, Table S2.1). Residuals of the reproductive weight–dorsal mantle length or mantle weight–dorsal mantle length relationship provide a size-independent measure of the condition of an individual at the whole animal level. Studentised residuals from the reproductive weight–dorsal mantle length and mantle weight–dorsal mantle length geometric average linear regression (Model II) equations were calculated (Table 3.1) using Box-Cox transformed variables to measure reproductive and somatic condition for each individual (Pecl & Moltschaniwskyj 2006). Individuals in better reproductive or somatic condition for their size will have positive residuals, i.e. more than the predicted values from the regression equation. Data was grouped by month to

determine how reproductive and somatic condition varied over the year. Austral seasons were identified as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November).

*Size and age at maturity*

Size (mantle weight) and age (days) at maturity were estimated as the mantle weight or age when 50% of the females and males were mature ($MW_{50\%}$ or $age_{50\%}$ respectively). This was estimated following Tafur *et al*. (2001) by creating a relative frequency distribution for size and age classes and fitting the results by the least-squares method to a logistic curve.

*Fecundity*

Three subsamples of ~50 eggs were randomly sampled from the centre of the ovaries, from halfway between the centre and the outer edge of the ovaries, and from the outer edge of the ovaries from immature and mature females. Remaining eggs were randomly subsampled from spent females. Each subsample was weighed and oocytes were counted and measured to 0.001 mm. Oocytes were classified to a developmental stage based on their external morphological characteristics (see Supporting information, Table S3.1). Potential fecundity was estimated by counting and averaging the number of oocytes in the three subsamples of known mass collected from the ovary, and extrapolating to the whole ovary mass. The frequency distribution of observed oocytes for every developmental stage was described at each maturity stage. The relative fecundity was estimated as the ratio of potential fecundity to mantle weight. The ratio of potential fecundity to eviscerated total

weight was also reported to facilitate comparison with previous studies. Actual fecundity was estimated as the difference between the average potential fecundity of mature females and the average potential fecundity of spent females. Maximum length of oocytes was used as a proxy of oocyte size.

*Oceanographic data*

Monthly SST and chlorophyll-*a* concentration (Chl-*a*) data for the area of collection were obtained and processed as per Chapter 2. *Octopus tetricus* was collected at shallow depths (35–46 m) where wind-driven mixing is high and tidal currents are strong (Sandery & Kämpf 2007); therefore SST was considered a valid temperature estimate of the habitats occupied by *O. tetricus*. Chlorophyll-*a* concentration is an estimator of primary productivity, often with strong links to biomass of higher trophic levels (Ware & Thomson 2005; Otero *et al*. 2008), and was therefore considered an indirect estimator of food availability for *O. tetricus*.

*Data analysis*

Weights and measurements of samples frozen at –20°C or preserved in 80% ethanol were adjusted as per Chapter 2 so they were comparable with fresh weights and measurements. Data transformation, and assumptions of normality and equality of variances were carried out as per Chapter 2. Where relevant, the Durbin–Watson statistic was used to test autocorrelation before correlations between reproductive-somatic condition of individuals, and SST or Chl-*a* concentration.

The temporal pattern of reproductive activity was defined on the basis of the reproductive condition, and frequencies of mature and spent individuals throughout

the year. Hence, Chi-square ($\chi^2$) goodness-of-fit tests were performed to assess whether the ratio of females to males (1:1), and the ratio of mature and spent individuals to immature individuals showed significant deviations throughout the year. Large differences between observed and expected values (studentised differences > 2) were identified when ratios were significantly different. A one-way ANOVA was used to test significant differences in average reproductive-somatic condition for females and males throughout the year, with a post hoc Tukey HSD test used to indicate where differences occurred. Pearson's correlation was used to describe the association between reproductive-somatic condition and SST or Chl-*a* concentration during the month of capture, as well as between potential fecundity and mantle weight, and potential fecundity and ovary weight. All statistics were carried out using R v. 3.0.1 (R Core Team 2013). Values presented in the text are average ± s.e.

Table 3.1 Summary of Model II linear regression statistics and 95% confidence intervals (CI) for Box-Cox transformed data of reproductive weight *v.* mantle length, and mantle weight *v.* mantle length relationships for *Octopus tetricus* from north-eastern Tasmania, Australia, during 2011

| Relationship of Mantle length to: | *n* | Slope | CI of slope | Intercept | CI of intercept | *P* | $r^2$ |
|---|---|---|---|---|---|---|---|
| Female | | | | | | | |
| Mantle weight | 233 | 1.09 | 1.01 to 1.19 | -2.12 | -3.06 to -1.90 | 0.009 | 0.72 |
| Reproductive weight | 233 | 0.46 | 0.48 to 0.50 | -4.08 | -4.48 to -3.68 | 0.009 | 0.71 |
| Male | | | | | | | |
| Mantle weight | 272 | 1.18 | 1.11 to 1.24 | -1.66 | -2.27 to -1.04 | 0.009 | 0.83 |
| Reproductive weight | 272 | 0.73 | 0.68 to 0.78 | -3.06 | -3.53 to -2.59 | 0.009 | 0.76 |

## Results

*Sex ratio and percentage of mature individuals*

The female : male ratio was significantly different throughout the year ($\chi^2$ = 21.35, *d.f.* = 6, *P* = 0.002), with approximately twice as many females as males during summer (Fig. 3.1). However, females were less common than males during the rest of the year (Fig. 3.1). Approximately 14% of the total number of females captured were mature or spent. The ratio of mature and spent to immature females was significantly different between months ($\chi^2$ = 32.6, *d.f.* = 6, *P* < 0.001), with a significantly greater percentage of mature or spent females sampled in summer (Fig. 3.2a). In addition, two females brooding eggs were found in the wild during summer and autumn. Mature or spent males were in greater proportion (44%) compared to mature and spent females and were significantly different between months ($\chi^2$ = 34.51, *d.f.* = 6, *P* < 0.001), with significantly greater percentages of mature-spent males during autumn and spring (Fig. 3.2b).

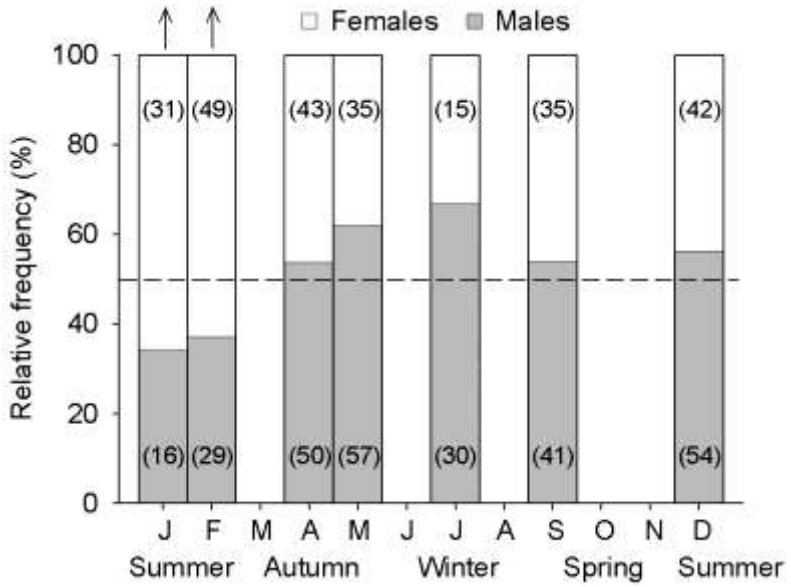


Figure 3.1 Relative frequency (%) of female and male *Octopus tetricus* collected off north-eastern Tasmania, Australia, during 2011. Pot lines were not retrieved by the commercial octopus fishers in March, June, August, October and November 2011. The horizontal dashed line indicates the sex ratio 1:1. Arrows pointing upward indicate the months when the percentage of females was significantly greater than the percentage of males. Number of individuals collected is in parentheses

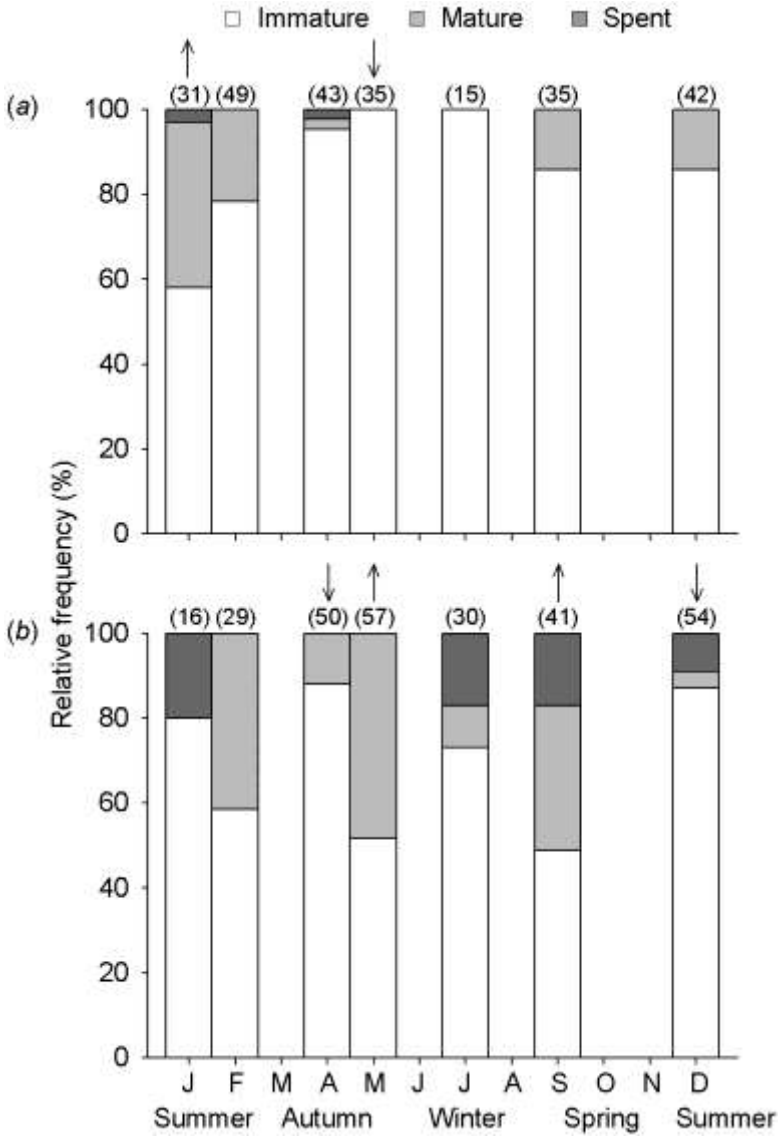


Figure 3.2 Relative frequency (%) of immature, mature and spent (*a*) female and (*b*) male *Octopus tetricus* from north-eastern Tasmania, Australia, during 2011. Pot lines were not retrieved by the commercial octopus fishers in March, June, August, October and November 2011. Arrows pointing upward indicate the months when the percentage of mature and spent individuals was significantly greater than the percentage of immature individuals. Arrows pointing downward indicate the months when the percentage of immature individuals was significantly greater than the percentage of mature and spent individuals. Number of individuals collected is in parentheses

*Reproductive-somatic conditions*

Average reproductive and somatic condition were significantly different between months for females (respectively $F_{(6,226)} = 44.29$, $P < 0.001$, and $F_{(6,226)} = 122$, $P < 0.001$) and for males (respectively $F_{(6,265)} = 40.85$, $P < 0.001$, and $F_{(6,265)} = 41.23$, $P < 0.001$). Females in better reproductive condition were observed mainly in summer and spring, whereas males in better reproductive condition were observed in summer, autumn, and spring (Fig. 3.3a, b). In contrast, females in better somatic condition were observed throughout the year, whereas males in better somatic condition were observed in autumn and spring (Fig. 3.3c, d). Reproductive condition of females was weakly negatively associated with SST ($r = –0.26$, $n = 233$, $P < 0.001$) and positively associated with Chl-*a* concentration ($r = 0.15$, $n = 233$, $P = 0.016$), whereas a stronger negative association was observed between somatic condition of females and SST ($r = –0.52$, $n = 233$, $P < 0.001$) and positive association with Chl-*a* concentration ($r = 0.47$, $n = 233$, $P < 0.001$). Similarly, strong negative associations were identified between reproductive and somatic condition of males and SST (respectively $r = –0.42$, $n = 272$, $P < 0.001$, and $r = –0.37$, $n = 272$, $P < 0.001$), and positive associations with Chl-*a* concentration (respectively $r = 0.45$, $n = 272$, $P < 0.001$, and $r = 0.55$, $n = 272$, $P < 0.001$).

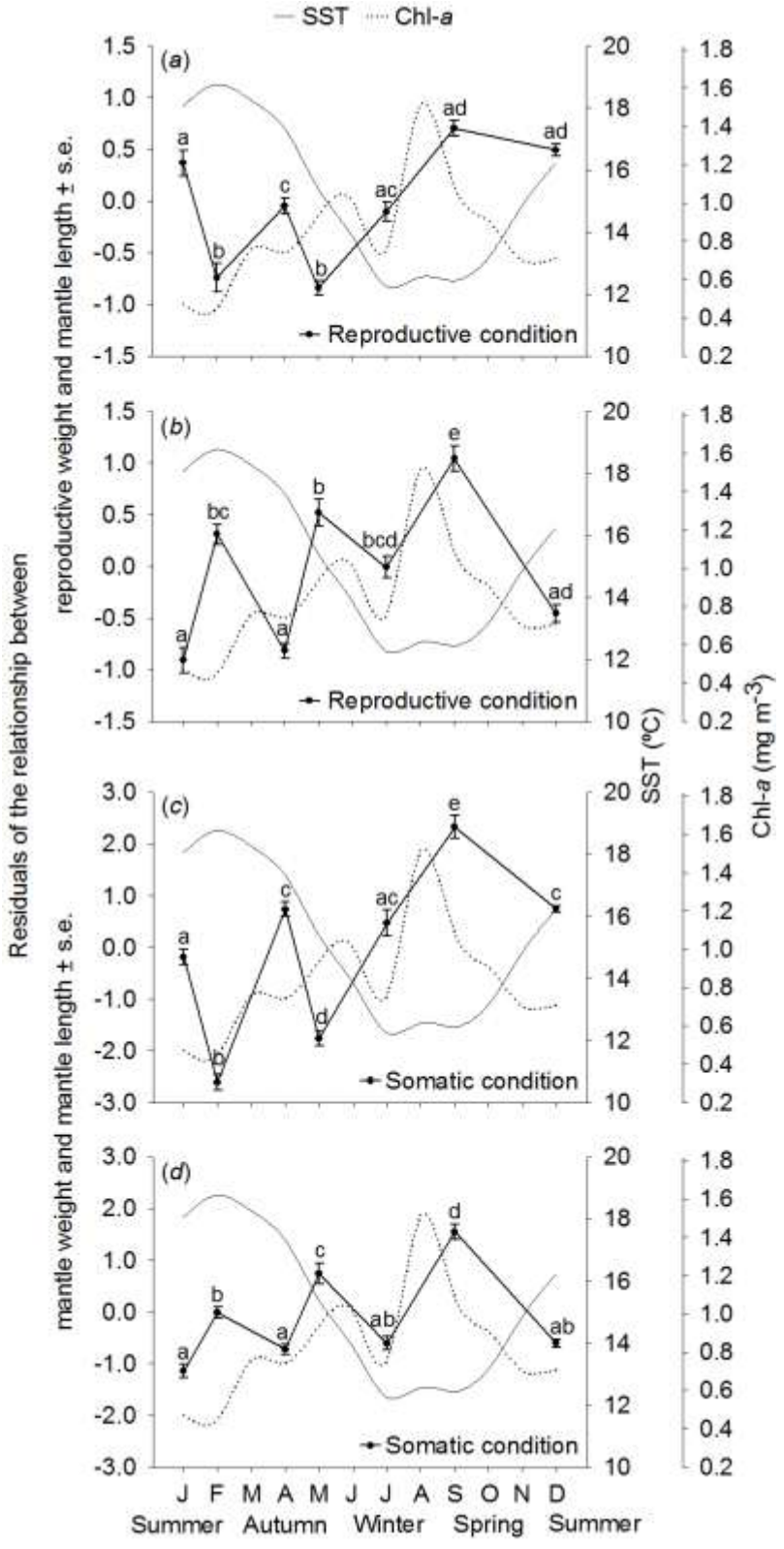


Figure 3.3 Monthly reproductive condition ± s.e. based on the relationship between reproductive weight and mantle length for (*a*) female and (*b*) male, and monthly somatic condition ± s.e. based on the relationship between mantle weight and mantle length for (*c*) female and (*d*) male *Octopus tetricus* from north-eastern Tasmania,

Australia, in relation to sea surface temperature (SST) (°C) and chlorophyll-*a* concentration (mg $m^{-3}$) during 2011. Samples were collected in January (*n* females = 31; *n* males = 16), February (*n* females = 49; *n* males = 29), April (*n* females = 43; *n* males = 50), May (*n* females = 35; *n* males = 57), July (*n* females = 15; *n* males = 30), September (*n* females = 35; *n* males = 41), and December (*n* females = 42; *n* males = 54). Pot lines were not retrieved by the commercial octopus fishers in March, June, August, October and November 2011. Mean condition indices with different letters are significantly different from each other

*Size-age at maturity and hatch schedule*

Females were, on average, 40 g heavier and 36 days older than males at maturity. Mantle weight at 50% maturity was 132 g for females and 92 g for males, whereas age at 50% maturity was 224 days for females and 188 days for males (Fig. 3.4). Individuals collected in this study were estimated to have hatched throughout the period March 2010 to September 2011 (Fig. 2.4 in Chapter 2), indicating that the population was composed of individuals from spawning events that occurred all year round.

*Fecundity*

Average potential fecundity was 283686 eggs ± 29830 s.e. for mature females and 5238 eggs ± 466 s.e. for spent females. Average relative fecundity in relation to mantle weight was 2333 eggs $g^{-1}$ ± 321 s.e. for mature females and 92 eggs $g^{-1}$ ± 88 s.e. for spent females. Average relative fecundity in relation to eviscerated total weight was 198 eggs $g^{-1}$ ± 29 s.e. for mature females and 7 eggs $g^{-1}$ ± 7 s.e. for spent females. Finally, average actual fecundity was 278448 eggs ± 29365 s.e. Potential fecundity was positively associated with mantle weight ($r$ = 0.50, $n$ = 35, $P$ = 0.002)

and ovary weight ($r$ = 0.53, $n$ = 35, $P$ < 0.001). Similarly, developmental stages of oocytes increased with maturity stage; i.e. previtellogenic oocytes were observed in ovaries of immature females. Ovaries of mature females had oocytes of every developmental stage, with most oocytes preparing for vitellogenesis, vitellogenic or ripe. Ovaries of spent females had mostly ripe eggs, although previtellogenic oocytes were also observed (Fig. 3.5). Average size (maximum length) of ripe eggs was 2.2 mm ± 0.1 s.e.

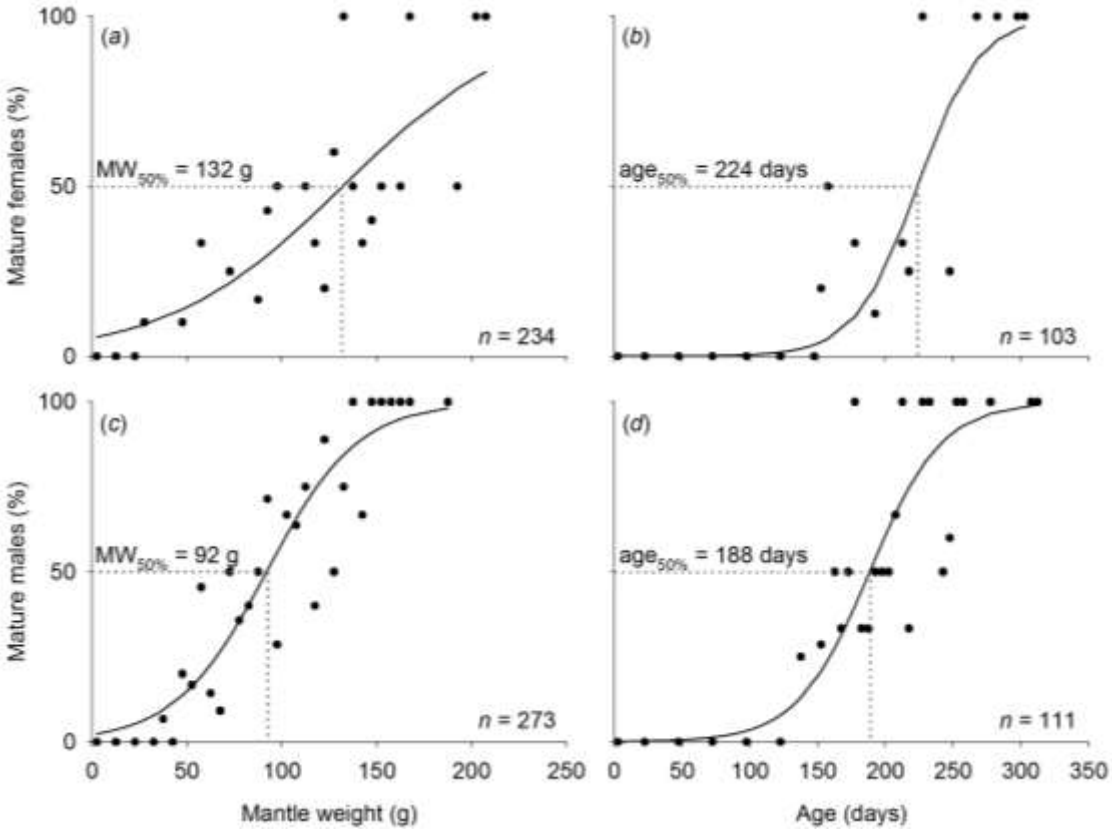


Figure 3.4 Size and age at 50% maturity (respectively $MW_{50\%}$ and $age_{50\%}$) for *Octopus tetricus* from north-eastern Tasmania, Australia, during 2011. (*a*) Mantle weight (g) and (*b*) age (days) at 50% maturity for females; (*c*) Mantle weight (g) and (*d*) age (days) at 50% maturity for males

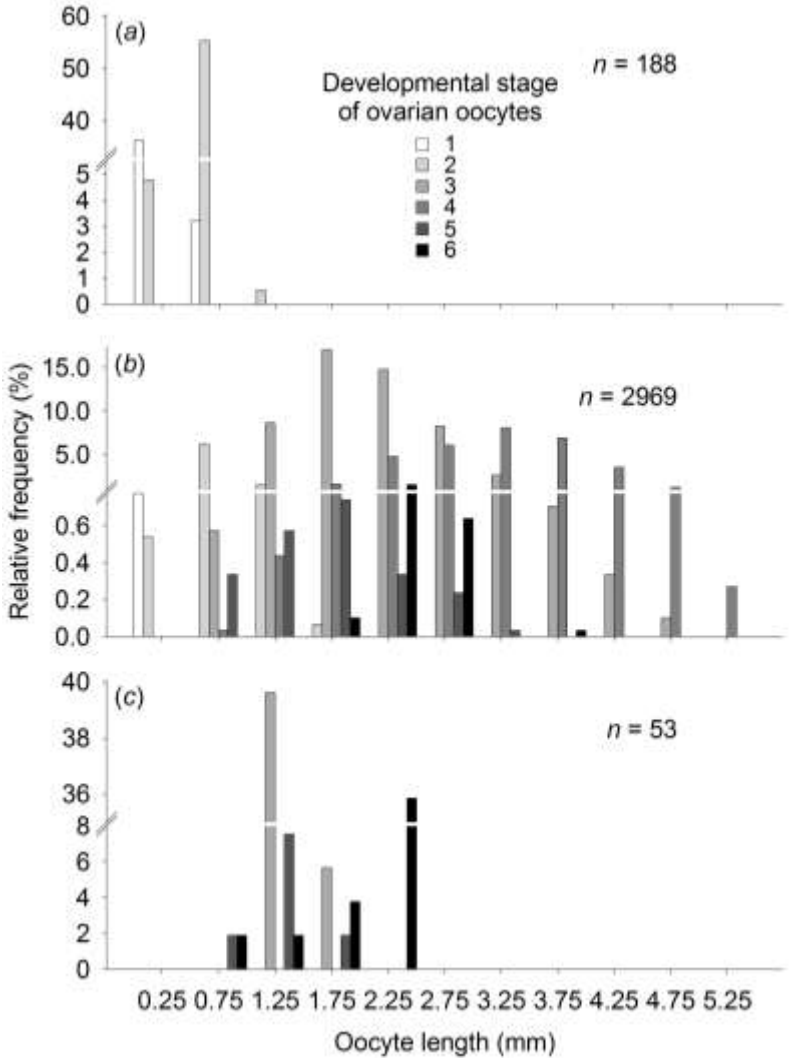


Figure 3.5 Relative frequency (%) distribution of developmental stage at size of ovarian oocytes of (*a*) immature, (*b*) mature, and (*c*) spent female *Octopus tetricus* from north-eastern Tasmania, Australia, during 2011. Oocyte developmental stages are: (1) second phase of previtellogenesis (PV), primary follicle; (2) third phase of PV, simple follicle; (3) phases of complicated follicle, formation of follicular folds, preparing for vitellogenesis (VG); (4) first and second phases of VG, vacuolization and yolk accumulation; (5) third phase of VG, expulsion of follicle folds; and (6) fourth phase of VG, ovulated ripe egg. *n*, observed number of oocytes. The ovaries of two immature, 29 mature, and two spent females were analysed

**Discussion**

This study reveals a range-extending species that is reproductively viable outside its historical range. Here it is demonstrated that the *O. tetricus* population inhabiting the range-extension area in Tasmanian waters is composed of the full range of life history stages, i.e. immature, mature and spent individuals. In addition, the population is sourced from spawning events occurring throughout the year, and the young age at maturity would promote a rapid population turnover. Furthermore, the high fecundity and advanced stages of oocyte development indicate that this species has a high reproductive potential and viability, which suggests that it has the potential to be a self-sustained population within the range-extension area. The reproductive characteristics of *O. tetricus* may thus facilitate its capacity to rapidly increase the size of the emerging population in the range-extension area, providing the offspring survive in the new habitats.

Populations at the limit of their distribution are exposed to environmental conditions that may affect their functional traits, including aspects of their reproductive biology (Pörtner & Farrell 2008). However, the presence of females brooding eggs in the wild in Tasmanian waters is additional evidence that *O. tetricus* is likely able to reproduce within the range-extension area. Furthermore, non-brooding females maintained in captivity successfully brooded viable hatchlings from May to October when reared at 13.7°C ± 1.6 s.d. ($n$ = 3), and in November at 15.9°C ± 1.7 s.d. (J.E. Ramos, G.T. Pecl, J.M. Semmens, J.M. Strugnell, R.I. León, N.A. Moltschaniwskyj, unpubl. data). This suggests that embryos can develop normally in the cool waters of Tasmania.

The back-calculated hatching frequency of individuals indicated that hatching events occur all year round. Individuals that hatched during productive conditions

would benefit by having access to increased biomass of food promoted by the cold and productive subantarctic waters that reach the east coast of Tasmania during late winter and spring (Harris *et al.* 1987; Rao & Huston 1995). Similar synchronies where hatchlings of cephalopods exploit greater availability of food during more productive conditions have been observed (Forsythe & Hanlon 1988; Kang *et al*. 2002; Richardson & Schoeman 2004; Pecl 2004; Pecl *et al*. 2004; Semmens *et al*. 2004; Otero *et al*. 2008). In this sense, the temporal pattern of reproductive activity of *O. tetricus* seems to be synchronised with the timing of favourable environmental conditions, potentially facilitating opportunities for the population to optimise resources within the range-extension area in north-eastern Tasmania.

The estimated frequency of hatched individuals presented is based on a non-systematic sampling scheme dependant on access to animals from a commercial fishery. Gaps in the collection of samples during some months in this study, in addition to stochastic mortality processes during the life span of octopus, will in part determine the observed frequency distribution of hatched individuals recorded. The temporal distribution of hatched individuals must therefore be interpreted with caution. A larger number of animals collected systematically and over a longer period are necessary to define the seasonal hatching patterns of *O. tetricus* with greater confidence. This would allow a better understanding of the link between the timing of reproductive events of *O. tetricus* and environmental conditions in the range-extension area. This study did not examine movement of animals associated with reproduction and very little is known about the patterns of distribution and abundance of *O. tetricus* in the range extension area, i.e. whether they occur inshore, offshore, and how far and how deep they occur offshore. With only data from animals collected through the fishery it was not possible make inferences about possible inshore/offshore

movements related to breeding as found in other octopus species off the Iberian peninsula (e.g. *Eledone cirrhosa* and *E. moscata*: Mangold-Wirz 1963) and off Japan (e.g. *Enteroctopus dofleini*: Rigby & Sakurai 2004 references therein).

*Octopus tetricus* reached maturity at a similar size compared to the closely related *O. vulgaris* (Silva *et al*. 2002; Oosthuizen & Smale 2003; Guzik *et al*. 2005; Otero *et al*. 2007). Potential fecundity estimated in this study for *O. tetricus* is similar to that of *O. vulgaris* from the Mediterranean with averages of 315197 oocytes ± 135865 s.d. (Silva *et al*. 2002) and 221447 oocytes ± 116031 s.d. (Otero *et al*. 2007), and greater than that of *O. maorum* (≤ 232000 larger eggs) from southern Australia (Grubert & Wadley 2000). In contrast, greater values (≤ 705000 eggs) have also been reported but in considerably larger individuals of *O.* cf. *tetricus* from Western Australia (Joll 1976) and *O. vulgaris* within their historical distributions (Silva *et al*. 2002; Oosthuizen & Smale 2003; Guzik *et al*. 2005; Otero *et al*. 2007). The average oocyte length for mature *O. tetricus* is consistent with oocyte sizes reported for *O. vulgaris* (3.0 mm ± 0.8 s.d.: Otero *et al*. 2007) and corresponds to the size of newly hatched paralarvae of *O.* cf. *tetricus* (total length 2.5 mm: Joll 1976) and *O. tetricus* (mantle length 2.1 mm ± 0.03 s.e.: J.E. Ramos, G.T. Pecl, J.M. Semmens, J.M. Strugnell, R.I. León, N.A. Moltschaniwskyj, unpubl. data). In addition, the presence of mature oocytes and ovulated eggs in the females suggests that eggs are successfully developing within the range-extension area. Overall, the reproductive capacity of *O. tetricus* does not seem to be limited by the cool waters off Tasmania; furthermore, the advanced stage of development of oocytes, and the number and size of oocytes that *O. tetricus* produces may allow it to be a self-sustaining population within the range-extension area.

The reproductive characteristics of *O. tetricus*, i.e. high fecundity, early maturity, and likely reproductive events all year round, may allow increasing reproductive effort within the range-extension area (Phillips *et al.* 2010). High reproductive effort (Simmons & Thomas 2004), in addition to fast growth rates and rapid population turnover (Ramos *et al.* 2014), promotes rapid population growth (Burton *et al.* 2010). These r-selected traits seem to be a strategy of colonist populations (McMahon 2002; Amundsen *et al.* 2012), for populations that grow fast are more likely to dominate available niches over populations of native species with low reproductive effort, long life spans, and low competitive ability (Burton *et al.* 2010). This advantage also has a genetic basis; for instance, genomes are copied more often per offspring produced. New positive gene complexes may thus result from greater numbers of produced offspring and when offspring are produced more frequently (Bromham 2011). These characteristics may facilitate the establishment and prevalence of the population in the range-extension area.

This study has highlighted the challenges and difficulties of examining life-history traits associated with populations undertaking range extensions associated with climate change. Although ideally larger numbers of individuals should be collected each month, population sizes at the range edge are often small (Bates *et al.* 2015), and knowledge of where populations have become established can limit the sample sizes, as experienced in this study. Reproductive characteristics observed in this study are likely to be typical for *O. tetricus* given that monthly SSTs off north-eastern Tasmania during 2011, year when samples were collected, were not atypical compared with monthly SSTs from other years, i.e. 2003–10. Reproductive activity throughout the years suggests that *O. tetricus* eggs may be able to survive the wide thermal window

of Tasmanian waters, even though eggs and larvae usually have narrow thermal limits (Pörtner & Farrell 2008).

*Octopus tetricus* appears to fulfil all aspects required for viable reproduction within the range-extension area. In summary, our findings suggest that *O. tetricus* is successfully reproducing within the range extension area; the size at maturity of individuals does not appear to be limiting its reproductive capacity, and the observed high fecundity suggests that it has the potential to be a self-sustaining population. Furthermore, reproductive events seem to be synchronized with environmental conditions during the year of study, which may promote survival and recruitment of paralarvae. Overall, this suggests that the reproductive capacity of *O. tetricus* is not compromised in the range-extension area, and it may actually facilitate the establishment and prevalence of the population beyond the historical distribution zone.

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# Chapter 4

## Population genetic signatures of a recent marine range extension

This chapter is submitted as:

**Ramos JE**, Pecl GT, Semmens JM, Moltschaniwskyj NA, Souza CA, Strugnell JM. Population genetic signatures of a recent marine range extension.

**Abstract**

Shifts in species distribution are one of the most commonly documented responses to ocean warming. The southwards extension of the warm East Australian Current has been associated with the recent shift in distribution of several dozen marine species along south-eastern Australia. One of these species is *Octopus tetricus* which has extended its distribution several hundred kilometres polewards. Knowledge of the level of connectivity, genetic structure and diversity among populations at the historical and extended range of distribution of a species is fundamental to identifying the genetic consequences of such range shifts. Therefore, seven microsatellite loci were used to examine the population connectivity, genetic structure and diversity of *O. tetricus* throughout its range. Significant genetic differences were detected between the historical distribution and the range extension zones. The population in the range extension zone was sub-structured and contained relatively high levels of self-recruitment, but was found to be sourced by migrants from along the entire geographic distribution. Levels of genetic diversity were comparable between the range extension zone and the historical distribution zone with no evidence of a bottleneck throughout its range. However, the estimated effective population size was smaller at the range extension zone compared to the historical distribution zone. The range extension of *O. tetricus* may be positively influenced by high gene flow from throughout the historical zone and by high genetic diversity, which may allow *O. tetricus* to cope with ocean warming by favouring adaptation, establishment, and likely long-term persistence in the range extension zone.

**Keywords:** Range shift, ocean warming, East Australian Current, cephalopod, *Octopus tetricus*, population establishment

## Introduction

In response to the accelerated warming of the oceans, many marine species experience changes in their patterns of geographic distribution and abundance as they track their preferred temperatures (Levitus *et al.* 2012; Sunday *et al.* 2012; Poloczanska *et al.* 2013). Such changes in geographic distribution and abundance, or range shifts, occur in the form of range contractions, relocations, or extensions, and are predicted to cause significant ecological and socio-economic impacts as the oceans continue to warm rapidly (Sorte *et al.* 2010; Madin *et al.* 2012). Maintaining genetic diversity is essential if populations are to sustain their adaptive potential and persistence as they undertake range shifts (Banks *et al.* 2010; Kanuch *et al.* 2014) and under accelerated global warming (Etterson & Shaw 2001). Most of our understanding on how genetic and evolutionary processes may relate to marine range shifts is based on terrestrial invasive or range shifting species (Davis & Shaw 2001; Drake 2006; Dlugosch & Parker 2008; Whitney & Gabler 2008; Kanuch *et al.* 2014; Signorile *et al.* 2014). However, compared with terrestrial species, marine species are exposed to a range of different barriers that influence the connectivity and genetic patterns of marine populations, e.g. water masses, currents, eddies, coastlines. Therefore the nature and magnitude of genetic patterns and evolutionary processes in marine species may differ from the terrestrial realm. Genetic patterns and evolutionary processes also can be difficult to examine in long-lived species in relation to the relatively recent accelerated ocean warming. In consequence, part of our knowledge on genetic patterns and evolutionary consequences of range shifts has been generated through theoretical studies (e.g. Edmonds *et al.* 2004; Excoffier *et al*. 2009; McInerny *et al*. 2009; Arenas *et al*. 2012) and only by a few empirical studies (e.g. Banks *et al.* 2010).

Genetic diversity is influenced by the reproductive exchange between individuals, the ability of individuals to disperse or migrate, the spatial and temporal scales at which dispersal or migration occurs, the presence of barriers to dispersal (Reichow & Smith 2001; Ray *et al*. 2003; Waples & Gaggiotti 2006), and the selection against poorly adapted genotypes (Davis & Shaw 2001). Genetic diversity can decrease due to genetic drift under scenarios of limited gene flow and genetic recombination (Davis & Shaw 2001). Genetic diversity also can decrease due to consecutive genetic bottlenecks or founder effects, where the size of the population is reduced for at least one generation or where only few individuals establish in new areas and subsequently become isolated (Austerlitz *et al*. 1997; Hallatschek & Nelson 2010). A population comprised of isolated individuals is at risk of undergoing genetic drift and inbreeding depression that negatively affect its adaptive potential and persistence (Signorile *et al.* 2014). However, there are exceptions where newly founded and eventually isolated populations overcome the negative impacts of low genetic diversity, known as the 'genetic paradox' (Roman & Darling 2007). The invasive long-spined sea urchin *Centrostephanus rodgersii* has sustained relatively high genetic diversity in range extension areas (Banks *et al.* 2010). Similarly, the genetic diversity of the colonizer Roesel's bush cricket *Metriptera roeselii* recovered rapidly in new areas (Kanuch *et al.* 2014). The sustained and rapidly recovered genetic diversity of *C. rodgersii* and *M. roeselii* respectively, were attributed to multiple introductions of individuals to the new areas, and to high mutation rates (Banks *et al.* 2010; Kanuch *et al.* 2014). Large numbers of individuals from diverse source areas that inter-breed in the new areas may increase genetic recombination, confer high phenotypic plasticity to the founder population, and strengthen its ability to respond to natural selection (Dlugosch & Parker 2008; Kanuch *et al*. 2014).

Sufficient mutation rates may counteract negative demographic effects and maintain beneficial mutations in the range extension areas (Bell & Collins 2008; Orr & Unckless 2008), where evolutionary rates may also increase because species are exposed to a new set of stressors (Whitney & Gabler 2008; Hoffmann & Sgrò 2011). In this sense, examination on the genetic structure of range shifting populations is important in order to assess the level of connectivity among populations and forecast successful range extensions as a function of gene flow (Signorile *et al*. 2014).

The southern Tasman Sea off Australia's east coast is warming up to 4 times faster than the global average (Poloczanska *et al.* 2007; Hobday & Pecl 2014), partly caused by the strengthening of the warm East Australian Current (EAC) which flows southwards from the southern Coral Sea along the south-east coast of mainland Australia (Ridgway & Dunn 2003). However, over the past 60 years the EAC has extended approximately 350 km further south towards the temperate east coast of Tasmania (Ridgway 2007; Hill *et al.* 2008). The strengthening of the EAC has been associated with the transport of several dozen marine species during their planktonic larval stage, and their subsequent polewards range shift (Johnson *et al*. 2011; Last *et al.* 2011). One of these range-shifting species is the gloomy or common Sydney octopus *Octopus tetricus* (Gould, 1852); this octopus has a short life span (~11 months; Ramos *et al.* 2014), high reproductive capacity (Ramos *et al*. 2015) and a planktonic paralarval phase. *Octopus tetricus* is closely related to *O. vulgaris* (Guzik *et al.* 2005; Amor *et al*. 2014), which planktonic paralarval phase is 35–60 days under laboratory conditions (Villanueva 1995; Carrasco *et al.* 2006). The historical geographic range of the commercially important *O. tetricus* is in shallow-waters from southern Queensland to southern NSW (Edgar 2000; Norman & Reid 2000; Rowling *et al*. 2010). However, the range extension of *O. tetricus* into Victorian and

Tasmanian waters, apparently after the years 2000 and 2006 respectively (Fig. 4.1), has been suggested based on systematic marine life censuses (Norman and Reid 2000; Edgar and Stuart-Smith 2014), fisheries records (Tasmania Department of Primary Industries and Water 2009), and citizen science monitoring using scientist-verified and geo-referenced photographs (REDMAP 2013). The range extension of *O. tetricus* is likely facilitated by the polewards transport of the planktonic paralarvae for up to 60 days by the EAC. Using a cost-effective rapid screening assessment tool based on monitoring data, Robinson *et al.* (2015) classified with "high" level of confidence the range extension of *O. tetricus*, and suggested that this species should be a priority when investigating potential ecosystem and socio-economic impacts in the extension area.

While *O. tetricus* from eastern Australia and from Tasmania are the same species (Amor *et al*. 2014), little is known about the population genetic structure of this species. Other merobenthic species of octopus in south-eastern Australia, *Macroctopus maorum*, is made up of populations with small but significant genetic differentiation, as shown by microsatellite markers (Doubleday *et al*. 2009). Microsatellite markers also allowed identifying limited gene flow, population structure and high heterozygosity of octopuses in different geographic regions, such as *O. vulgaris* in the Iberian peninsula and Brazil (Cabranes *et al*. 2008; Moreira *et al.* 2011), and *Pareledone turqueti* around Antarctica (Strugnell *et al*. 2012). Given the apparently recent range extension of *O. tetricus*, I predict that this species has not yet experienced population subdivision, but it may have experienced a reduction in genetic diversity in the range extension area. This study provides an opportunity to examine the population genetic structure and genetic signatures of a marine species undergoing a range extension. The aims of this study are 1) to determine the

population genetic structure of *O. tetricus* along eastern Australia, including historical and extension areas, 2) to determine the level of gene flow between historical and range extension areas, 3) to identify the source populations that are contributing to the range extension of *O. tetricus*, 4) to quantify the genetic diversity of the range extension *vs* other population components, and 5) to determine if there is evidence of a bottleneck effect or demographic effect that may negatively affect the persistence of *O. tetricus* at extended areas. This study will help identify how early genetic signatures relate to the capacity of a marine species to establish and persist in new areas.

## Material and methods

### *Specimen collection*

Octopuses were collected from inshore waters along the NSW coast at Nambucca Heads (*n* = 17; 30°38'46"S, 153°0'12"E) and Swansea (*n* = 30; 33°5'9"S, 151°38'20"E) during February 2014; and at Ulladulla (*n* = 5; 35°19'20"S, 150°31'29"E), Merimbula (*n* = 29; 36°53'42"S, 149°54'25"E), and Eden (*n* = 8; 37°4'18"S, 149°54'33"E) during May 2013. Sites along the Victorian coastline were Mallacoota (*n* = 29; 37°33'22"S, 149°45'36"E) and Cape Conran (*n* = 3; 37°48'49"S, 148°43'37"E) with samples collected during May 2013. Samples also were collected off north-eastern Tasmania (*n* = 61; 39°43'36"S, 148°27'17"E) during April, September and December 2011. The centre of the known historical distribution included Nambucca Heads, Swansea, and Ulladulla; sites at the polewards edge of the historical distribution were Merimbula and Eden, whereas sites at the range extension zone were Mallacoota, Cape Conran, and Tasmania (Fig. 4.1). Octopuses from

Tasmania were collected on board of the commercial *FV Farquharson* using black plastic shelter pots (0.3-m long × 0.1-m high × 0.1-m wide) laid on the seafloor at depths of 35–46 m. Octopuses were euthanized by commercial fishers and immediately put in watery ice in an insulated container to maintain the specimens at low temperature and avoid exposure to the sun. A tissue sample was taken from the arm or mantle of every specimen and octopus carcasses were returned to the fishers. Octopuses from Ulladulla were collected during diving activities whereas specimens from all other sites along the coast of mainland Australia were collected by hand while snorkelling at depths of 1–3 m. These animals were anesthetised by immersion in a 2% $MgCl_2$ solution, a tissue sample was taken and octopuses were released after recovery. All tissue samples were fixed in 95% ethanol.

*DNA extraction, PCR amplification and genotyping*

DNA was extracted using the high salt method (Sambrook *et al.* 1989) from a total of 182 animals. Seven microsatellite primers (Table 4.1) identified by Zuo *et al.* (2012) for *O. vulgaris* were amplified in *O. tetricus* and found to be polymorphic. Microsatellite loci were assigned unique fluorophores (FAM, VIC, NED, PET) following Blacket *et al*. (2012) to enable fluorescent tagging of PCR products.

PCR reactions were performed following the reaction conditions of Zuo *et al.* (2012), with modifications to the annealing temperature (Ta) (Table 4.1). Each PCR contained 4.725 µL of double distilled $H_20$, 6.25 µL of MyTaq Redmix (Bioline), 0.075 µL of 10mM forward primer, 0.25 µL of 10mM reverse primer, 0.20 µL of 5pmol/µL fluorophore labelled primer, and 1 µL (18–37 ng) of DNA. PCR conditions were modified slightly to optimize PCR products for some samples, such that 1 µL of 25mM $MgCl_2$ (Promega) was added in place of water. In addition, the number of

cycles was reduced from 35 to 30, and the final extension was reduced from 5 to 3 mins. Capillary separation of PCR products was performed by the Australian Genome Research Facility Ltd (AGRF). Two trained persons independently scored genotypes by eye using Geneious Pro v. 5.6.4 (Drummond *et al.* 2012). PCRs were repeated up to three more times for individuals with unclear or missing single-locus genotypes before being categorized as missing data and scored as 0 ($n$ = 25).

*Genetic polymorphism*

Micro-Checker v. 2.2.3 (Van-Oosterhout *et al.* 2004) found no evidence of large-allele dropout; stuttering was suggested for loci Ovul02 and Ovul16, as indicated by the shortage of heterozygote genotypes with alleles of one repeat unit difference. FreeNA (Chapuis & Estoup 2007) estimated moderate levels of null alleles in loci Ovul01 (10%), Ovul02 (14%), Ovul05 (≤19%), and Ovul16 (≤13%). High frequencies of null alleles are commonly observed in marine invertebrate species including molluscs (Li *et al* 2003; Kaukinen *et al.* 2004; Astanei *et al.* 2005). The presence of null alleles can lead to overestimation of $F_{ST}$ in cases of low levels of gene flow and significant population differentiation. Therefore null alleles were corrected by re-naming them as 999, which greatly reduces the bias caused regardless of the frequency of null alleles, the level of gene flow, and the number of loci (Chapuis & Estoup 2007). There were differences in the results estimated from original and corrected data, therefore we present and discuss results based on corrected data.

Table 4.1 Variability across seven polymorphic microsatellite loci in *Octopus tetricus* from the east coast of Australia

| Locus | Accession number | Repeat motif | Primer sequence (5'–3') | Ta (ºC) | Size range (bp) | $N_A$ | $H_O$ | $H_E$ |
|---|---|---|---|---|---|---|---|---|
| Ovul01 | JN579690 | $(TG)_{15}N(TG)_6N(TG)_6$ | AGATGAGGCAAAAGCAGAATA | 65 | 252–263 | 7.8 | 0.680 | 0.749 |
| | | | GAATGACTTCATAAAGCCACCT | | | | | |
| Ovul02 | JN579691 | $(GC)_4N(AC)_{31}$ | ACTGCCTGCCACTGTCTC | 65 | 251–302 | 24.6 | 0.847 | 0.956 |
| | | | ATTTGATTTACTCACATCGGGTT | | | | | |
| Ovul05 | JN579694 | $(AG)_4N(GA)_6N(TG)_5N(AG)_5AA(AG)_8$ | GGAAGGAGAAGGACGAGAG | 65 | 235–263 | 7.2 | 0.328 | 0.427 |
| | | | CCTCCCACGAACACTCAT | | | | | |
| Ovul08 | JN579697 | $(AC)_5N(CA)_{10}N(AC)_8N(TC)_8N(TC)_4$ | CCGTCAGATTATGCCAACAC | 67 | 322–345 | 4.8 | 0.351 | 0.340 |
| | | | GCGAGTGAAGGGGAAGTAGA | | | | | |
| Ovul09 | JN579698 | $(GT)_{20}(GA)_{18}N(GA)_4$ | GGAAGGAATAAGAACAGAGAACG | 62 | 367–397 | 14.2 | 0.863 | 0.894 |
| | | | ATCTCTAATCTTCATTGCGTCTAA | | | | | |
| Ovul14 | JN579703 | $(GT)_4GCT(TG)_{31}N(GT)_5N(TG)_4$ | GGTGGGTGGCTGGTTTGACTACC | 60 | 261–282 | 8.8 | 0.735 | 0.810 |
| | | | CACTCAGGCAAATAGGGAAC | | | | | |
| Ovul16 | JN579705 | $(GT)_8GCA(TG)_4$ | AAGGGGCTGGTGACATTG | 65 | 148–158 | 4.2 | 0.323 | 0.363 |
| | | | CACTGGCATACTACATCAAACC | | | | | |

Ta, annealing temperature; $N_A$, number of alleles; $H_O$, observed heterozygosity; $H_E$, expected heterozygosity. Microsatellite loci modified from Zuo *et al.* (2012)

*Population structure*

The Discriminant Analysis of Principal Components (DAPC) (Jombart *et al.* 2010) was used with the 'adegenet' package (Jombart 2008) in R v. 3.0.1 (R Core Team 2013) to test separately for sub-structure of *O. tetricus* along the east coast of Australia, at all sites within mainland Australia, at the historical distribution only, at the range extension zone only, and from within Tasmania. In addition, the admixture model (assuming some level of connection between all sites) was implemented using Structure v. 2.3.4 (Pritchard *et al*. 2000) to examine the population structure of *O. tetricus* along the east coast of Australia. The number of clusters (K) explored was 1–10, with 5 independent runs of 500,000 Monte Carlo Markov Chain (MCMC) replicates and 30 iterations; a burnin length of 50,000 was selected. The Evanno method (Evanno *et al*. 2005) implemented within Structure Harvester v. 0.6.93 (Earl & vonHoldt 2012) was used to evaluate the results, which were graphically displayed using Distruct v. 1.1 (Rosenberg 2004).

*Phylogenetic analysis*

Partial sequences of 650 bp of the mitochondrial gene Cytochrome Oxidase subunit I (COI) were targeted in 25 µL reactions comprised of 12.5 µL MyTaq Red Mix (Bioline), 0.5 µl forward primer LCO (10 µM), 0.5 µL reverse primer HCO (10 µM), 9.5 µL dd$H_2O$, and 2 µL DNA (10–30 ng/µL). Reaction conditions were a denaturation step of 95°C for 2 min, followed by 35 cycles of 95°C for 30 s, 48°C for 30 s, and 72°C for 30 s, and a final extension step of 72°C for 5 min. PCR products were sequenced by Macrogen Inc. (Seoul, Korea). A phylogenetic tree was constructed with a set of subsamples to corroborate that individuals of different groups

(Ot1 and Ot2) were both *O. tetricus*. jModelTest v. 0.1.1 (Posada 2008) was used to carry out statistical selection of best-fit models on the basis of goodness of fit measure using the Akaike Information Criterion (Akaike 1974). Topologies were constructed via Maximum Likelihood using PhyML v. 3.1 (Guindon *et al.* 2010). Searches were undertaken and model parameter values were estimated; 1000 bootstrap replicates were used to measure the strength of support for internal nodes. Bayesian marginal posterior probabilities were calculated using MrBayes v. 3.2 (Ronquist & Huelsenbeck 2003). Parameters of the model were estimated; trees were started randomly and the analysis was run for 15 million generations, with samples of the Markov chain every 1000 generations. Convergence of the Markov chain and appropriate 'burn-in' length were assessed using Tracer v. 1.6 (Rambaut *et al*. 2013).

*Genetic connectivity and differentiation*

Pairwise $F_{ST}$ was calculated using FSTAT v. 2.9.3 (Goudet 1995) between all individuals from the historical distribution zone against all individuals from the range extension zone, and pairwise comparisons between all sites with ≥17 samples. A Mantel matrix correlation test was performed in GENEPOP web v. 4.2 (Raymond & Rousset 1995; Rousset 2008) to examine if genetic differentiation ($F_{ST}$) was explained by isolation by geographical distance (km) between collection sites (excluding Ulladulla, Eden, and Cape Conran with <17 samples). Isolation by year of collection was also tested for collection sites, i.e. 2011 (Tasmania), 2013 (Mallacoota and Merimbula), and 2014 (Swansea and Nambucca Heads). In addition, AMOVA implemented in Arlequin v. 3.5.1.3 (Excoffier & Lischer 2010) was used to test for hierarchical partitioning of genetic variation among sampling sites, and groups detected by DAPC and Structure.

*Migration and self-recruitment*

BayesAss v. 3.0.1 (Wilson & Rannala 2003) was used to assess admixture (Faubet *et al*. 2007). 50,000,000 iterations and a 10,000,000 burnin length were used to produce convergent trace outputs. Trace output convergence was assessed using Tracer v. 1.6 (Rambaut *et al*. 2013). Migration rates and inbreeding coefficients were estimated between the historical distribution (Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden pooled) and the range extension (Mallacoota, Cape Conran, and Tasmania pooled) zones, as well as between each site.

*Genetic diversity*

Descriptive statistics were estimated for all pooled sites from within the historical distribution zone (Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden) and from the range extension zone (Mallacoota, Cape Conran, and Tasmania). Descriptive statistics were also estimated for each collection site where ≥17 individuals were collected. Genepop was used to test for genotypic linkage disequilibrium among loci within sites, and for departures from Hardy–Weinberg equilibrium using the score test for heterozygote deficiency with level of significance determined by the Markov chain method. The number of private alleles ($N_{PA}$) was calculated using Convert v. 1.31 (Glaubitz 2004). The number of alleles ($N_A$), allelic richness ($A_R$) standardized to 17 samples and inbreeding coefficient ($F_{IS}$) was calculated using FSTAT.

*Bottleneck analysis*

Evidence for a genetic bottleneck was tested with the software Bottleneck v. 1.2.02 (Cornuet *et al*. 1999), using 1,000 iterations for the historical distribution (Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden pooled) and for the range extension (Mallacoota, Cape Conran, and Tasmania pooled) zones, and for each site with ≥17 samples. Four different tests were used: i) The "sign test" for heterozygosity excess (Luikart & Cornuet 1998), ii) the "standardized differences test" for differences in allele frequencies (Cornuet & Luikart 1996), iii) the "Wilcoxon test" for reduced mean heterozygosity (Luikart *et al.* 1998), and iv) the "mode-shift qualitative test" for distortion of allele frequency distributions (Luikart *et al.* 1997). Loci used in this study are likely to evolve under the Infinite Allele Mutation model (IAM; Kimura & Crow 1964). However, the Stepwise Mutation model (SMM; Ohta & Kimura 1973) is more conservative, therefore both mutation models were considered in this analysis.

*Effective population size*

$N_E$Estimator v. 2 (Do *et al.* 2014) was used to estimate effective population size (Ne) for historical distribution and range extension zones, and for each site with ≥17 samples using the linkage disequilibrium method. These results must be interpreted with caution because the collection design did not account for an individual's reproductive status, age structure, or immigration which may bias Ne (Charlesworth 2009; Luikart *et al.* 2010; Palstra & Fraser 2012).

## Results

A total of 182 individuals of the common Sydney octopus *Octopus tetricus* were genotyped for seven microsatellite loci. Approximately 96% of pairs of loci (of 105 tests over sites with ≥17 samples) were in linkage equilibrium. The 4% of pairs of loci in linkage disequilibrium ($P < 0.05$) occurred only at Mallacoota and Tasmania (10% of Mallacoota's and 10% of Tasmania's pairs of loci were in linkage disequilibrium; Table S4.1, Supporting information); therefore all loci were included in further analyses. Hardy-Weinberg equilibrium was met in 77% of each of the site-locus comparisons (Table S4.2, Supporting information).

### *Population structure*

DAPC identified five clusters where clusters one (purple), two (green), three (blue) and five (orange) were comprised of individuals from sites at the historical and extended areas (Fig. 4.1). Of these, very few individuals were assigned to single clusters. Clusters one to three, and cluster five were common along the entire distribution and were termed group Ot1 (Fig. 4.1). Cluster four (red) was mostly comprised of individuals from Tasmania in the range extension zone ($n = 26$), but also contained a few individuals from Nambucca Heads ($n = 1$), Swansea ($n = 2$) and Merimbula ($n = 2$) in the historical distribution zone (Table 4.2, Fig. 4.1). Tasmania was thus sub-structured with 59% individuals that belonged to the common group Ot1, and with 41% individuals that belonged to the genetically distinct group termed Ot2. DAPC analyses carried out on a range of subsets of the dataset (mainland Australia only, the historical distribution zone, the range extension zone, Tasmania only, and repeated after removing the distinct group Ot2) showed the same population structure. Structure analyses detected only four clusters; individuals in cluster five

detected by DAPC were equally assigned to clusters one to three by Structure (Table 4.2, Fig. 4.2).

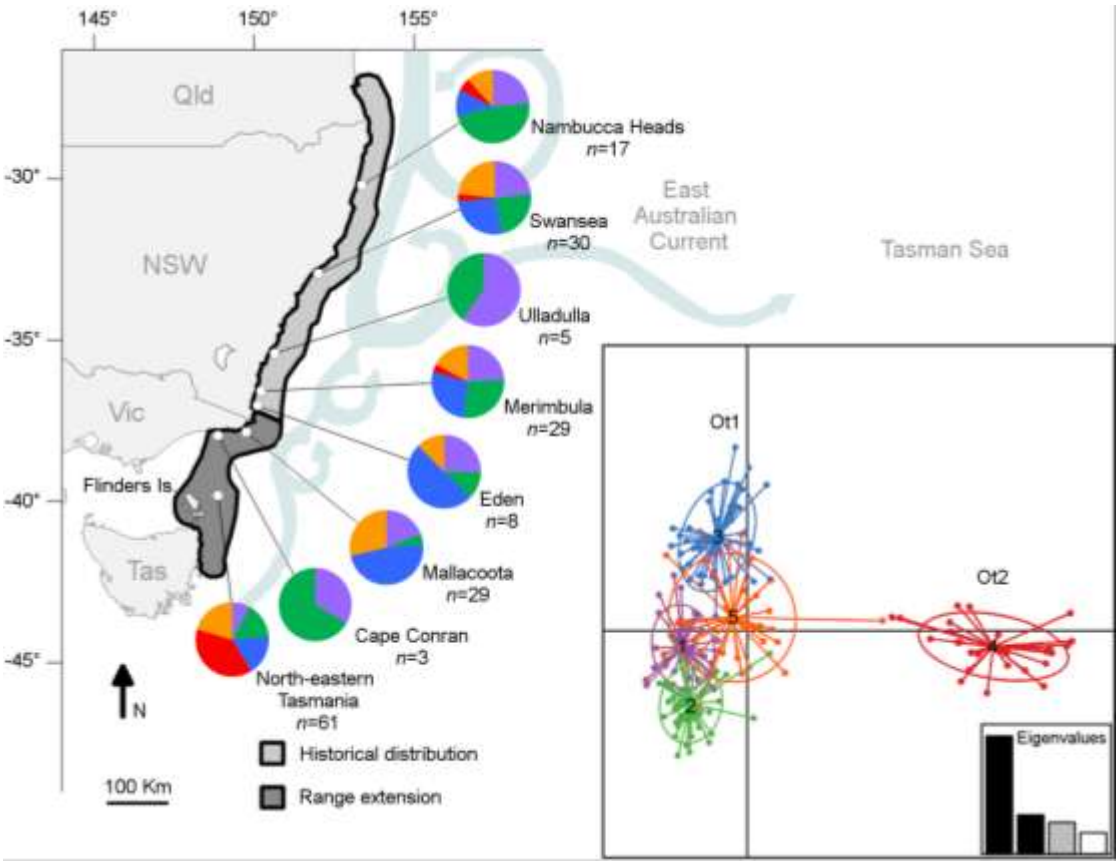


Figure 4.1 Collection sites for *Octopus tetricus* along eastern Australia, including historical and extension zones. The pie charts indicate the percentage of individuals from each site that correspond to each cluster assigned by colour (cluster 1 = purple; cluster 2 = green; cluster 3 = blue; cluster 4 = red; cluster 5 = orange), and identified with the Discriminant Analysis of Principal Components (right panel). Cluster 1) Individuals from all sites with greater percentage from Ulladulla; Cluster 2) Individuals from all sites with greater percentage from Cape Conran and Nambucca Heads; Clusters 3) Individuals from all sites, except from Ulladulla and Cape Conran; Cluster 4) Individuals from Tasmania with little percentage from Nambucca Heads, Swansea, and Merimbula; Cluster 5) Individuals from all sites, except from Ulladulla and Cape Conran. Clusters 1, 2, 3, and 5 comprise the common group Ot1. Cluster 4 comprises the distinct group Ot2 (red cluster in Figure 4.2)

Table 4.2 Percentage (%) contribution of *Octopus tetricus* individuals from the east coast of Australia to assigned clusters estimated in DAPC and Structure

| Site | DAPC | | | | | Structure | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 |
| Nambucca Heads | 23.5 | 47.1 | 11.8 | 5.9 | 11.8 | 33.7 | 28.3 | 33.7 | 4.4 |
| Swansea | 23.3 | 23.3 | 26.7 | 3.3 | 23.3 | 31.3 | 29.3 | 31.5 | 7.9 |
| Ulladulla | 60.0 | 40.0 | 0.0 | 0.0 | 0.0 | 46.6 | 4.3 | 47.4 | 1.7 |
| Merimbula | 24.1 | 27.6 | 27.6 | 3.4 | 17.2 | 33.4 | 23.7 | 33.7 | 9.2 |
| Eden | 25.0 | 12.5 | 50.0 | 0.0 | 12.5 | 31.9 | 31.2 | 32.4 | 4.5 |
| Mallacoota | 13.3 | 3.33 | 33.3 | 0.0 | 20.0 | 32.0 | 30.1 | 31.7 | 6.2 |
| Cape Conran | 33.3 | 66.7 | 0.0 | 0.0 | 0.0 | 29.5 | 35.0 | 29.8 | 5.7 |
| Tasmania | 7.9 | 15.9 | 17.5 | 38.1 | 20.6 | 20.1 | 22.5 | 19.9 | 37.5 |

DAPC, Discriminant Analysis of Principal Components. Cluster one = purple; cluster two = green; cluster three = blue; cluster four = red, and cluster five = orange in figures 4.1 and 4.2

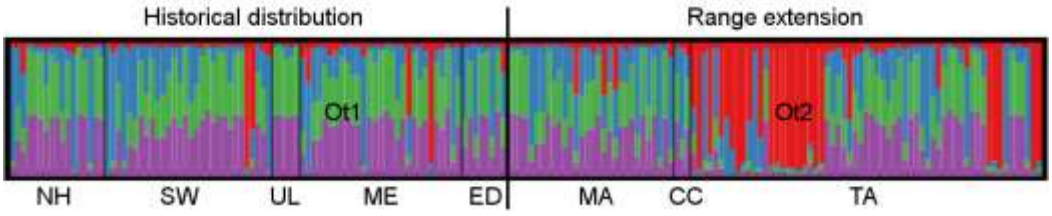


Figure 4.2 Identification of clusters for individual *Octopus tetricus* from the east coast of Australia using Structure. The percentage of contribution of individuals (columns) to identified clusters (K = 4) is indicated by four colours respectively. Cluster 1 = purple; cluster 2 = green; cluster 3 = blue; cluster 4 = red. Sites of collection are separated by thin black lines. Historical distribution zone: NH, Nambucca Heads; SW, Swansea; UL, Ulladulla; ME, Merimbula; ED, Eden. Range extension zone: MA, Mallacoota; CC, Cape Conran; TA, north-eastern Tasmania; Ot1, Individuals that are common along the east coast of Australia (mixed of purple, green, and blue); Ot2, cluster 4 mostly comprised of individuals from Tasmania with few individuals from Nambucca Heads, Swansea, and Merimbula (red). Historical distribution and range extension zones are separated by thick black line

*Phylogenetic analysis*

Sequences of the mitochondrial gene COI demonstrated that individuals of the groups Ot1 and Ot2 are *O. tetricus* (Fig. 4.3).

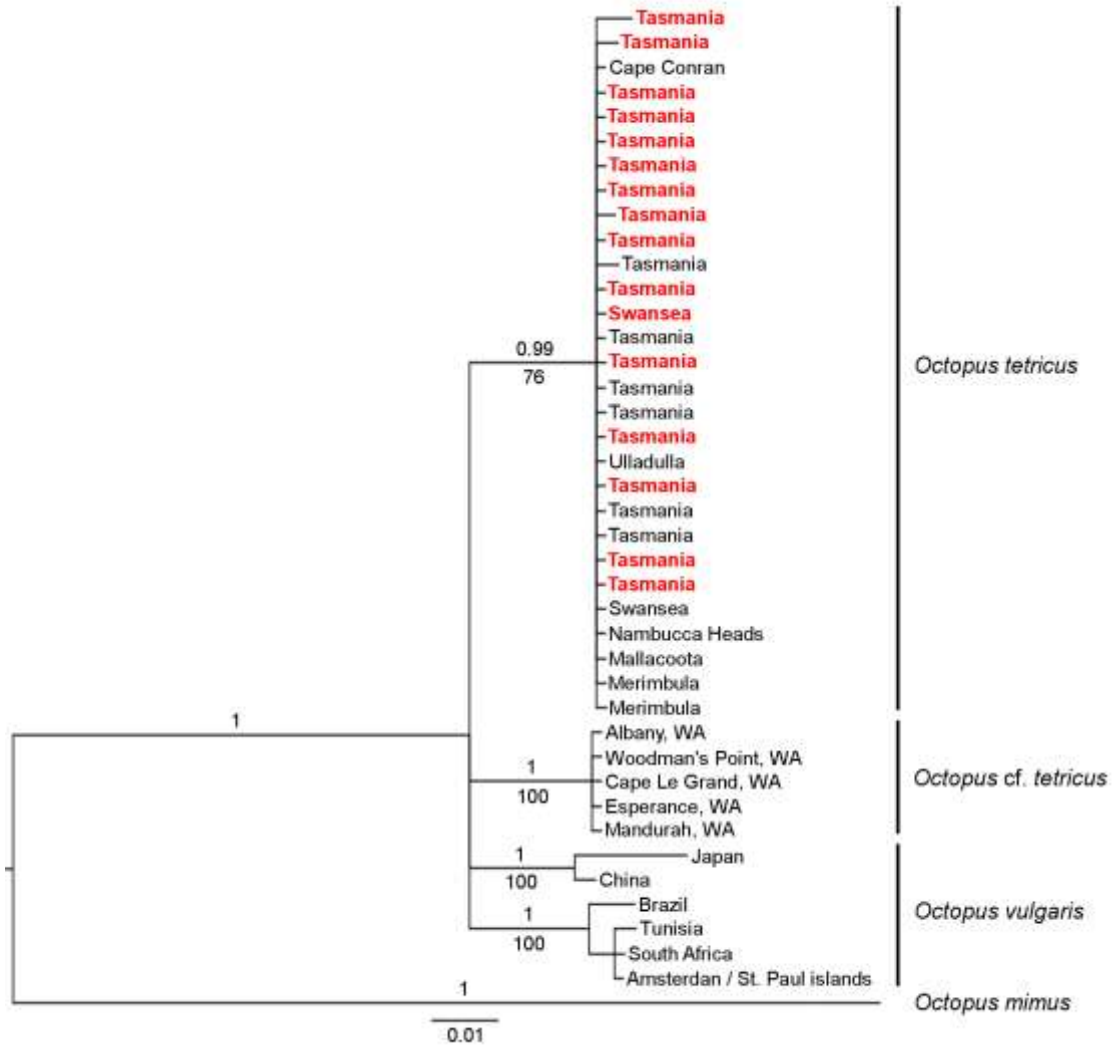


Figure 4.3 Bayesian and Maximum Likelihood topologies of *Octopus tetricus* from along eastern Australia compared to genetically close species *Octopus* cf. *tetricus* and *Octopus vulgaris*. Phylogenetic analysis is based on the mitochondrial gene COI. Bayesian posterior probabilities and maximum likelihood bootstrap values are indicated above and below the branches respectively. Outgroup is *Octopus mimus*. Node labels indicate the location of each individual. *Octopus tetricus* individuals belonging to group Ot1 are in normal text. *Octopus tetricus* individuals belonging to group Ot2 are in bold red text. WA. Western Australia

*Genetic connectivity and differentiation*

Genetic differentiation calculated in FSTAT was found to be significant between all individuals from the historical distribution and all individuals from the range extension zones ($F_{ST}$ = 0.0199, $P$ = 0.05). The $F_{ST}$ comparison among sites showed that the distinct group Ot2 was significantly different to any other site including the rest of individuals from Tasmania (Ot1). The Tasmanian component of the group Ot1 also was significantly different to octopuses from all other sites except for Mallacoota, whereas Mallacoota was significantly different to Swansea (Table 4.3). The Mantel test indicated that geographic distance did not influence the level of genetic differentiation among collection sites ($P$ = 0.258). There was no significant correlation between genetic differentiation and year of collection among collection sites ($P$ = 0.096).

The AMOVA detected significant percentages of genetic variation among sites within historical distribution and the range extension areas (2.9%, $P$ < 0.001), and among sites within the groups Ot1 vs Ot2 group (4.5%, $P$ < 0.001).

*Migration and self-recruitment*

Migration rates were asymmetric between the historical distribution zone and the range extension zone. Greater migration rates were detected from the historical distribution zone towards the range extension (0.237 ± 0.018 s.d.), than from the range extension towards the historical distribution zone (0.036 ± 0.013 s.d.). Migration rates were also notably asymmetric between Mallacoota and all other sites. Migration rates were high from Mallacoota to the sites in the historical distribution zone and towards the Tasmanian component of Ot1 (0.256 ± 0.028 s.d.; Table 4.4). It is important to note that the accuracy of BayesAss is reduced when estimating migration rates

between sites with low genetic differentiation ($F_{ST} \leq 0.05$) (Faubet *et al*. 2007). This may be particularly reflected in the very low migration rates detected between sites at the historical distribution zone. The highest levels of self-recruitment were detected at the range extension, in particular at the distinct group Ot2 (0.910 ± 0.026 s.d.) and at Mallacoota (0.796 ± 0.043 s.d.).

Table 4.3 $F_{ST}$ among collection sites for *Octopus tetricus* along the east coast of Australia

| Site | Nambucca Heads | Swansea | Merimbula | Mallacoota | Tasmania |
|---|---|---|---|---|---|
| Swansea | 0.0005 | | | | |
| Merimbula | 0.0026 | 0.0001 | | | |
| Mallacoota | 0.0182 | **0.0117** | 0.0126 | | |
| Tasmania | **0.0173** | **0.0083** | **0.0051** | 0.0051 | |
| Tasmania (Ot2) | **0.1609** | **0.1380** | **0.1336** | **0.1648** | **0.1314** |

Historical distribution zone: Nambucca Heads, Swansea, and Merimbula. Range extension zone: Mallacoota and north-eastern Tasmania. The common group Ot1 indicated in the text is comprised of individuals from all sites. The distinct group Ot2 is predominately comprised of individuals from Tasmania (red cluster in figures 4.1 and 4.2). Bold indicates significant values after Bonferroni correction of $P < 0.005$. $F_{ST}$ was not estimated for Ulladulla, Eden and Cape Conran due to their small sample sizes ($n$ <17)

Table 4.4 Migration rates (posterior probabilities) of *Octopus tetricus* between collection sites along the east coast of Australia

| Site | Nambucca Heads | Swansea | Ulladulla | Merimbula | Eden | Mallacoota | Cape Conran | Tasmania | Tasmania (Ot2) |
|---|---|---|---|---|---|---|---|---|---|
| Nambucca Heads | *0.680 (0.013)* | 0.013 (0.013) | 0.013 (0.013) | 0.014 (0.013) | 0.013 (0.012) | 0.210 (0.031) | 0.013 (0.013) | 0.021 (0.018) | 0.025 (0.018) |
| Swansea | 0.009 (0.009) | *0.676 (0.009)* | 0.009 (0.008) | 0.009 (0.008) | 0.009 (0.009) | 0.237 (0.026) | 0.009 (0.008) | 0.019 (0.016) | 0.025 (0.016) |
| Ulladulla | 0.024 (0.022) | 0.024 (0.022) | *0.692 (0.023)* | 0.024 (0.022) | 0.024 (0.022) | 0.142 (0.042) | 0.024 (0.022) | 0.024 (0.022) | 0.024 (0.022) |
| Merimbula | 0.009 (0.009) | 0.009 (0.009) | 0.009 (0.009) | *0.676 (0.009)* | 0.009 (0.009) | 0.236 (0.026) | 0.009 (0.009) | 0.016 (0.013) | 0.028 (0.016) |
| Eden | 0.020 (0.019) | 0.020 (0.019) | 0.020 (0.019) | 0.020 (0.019) | *0.687 (0.019)* | 0.170 (0.040) | 0.020 (0.019) | 0.024 (0.023) | 0.020 (0.019) |
| Mallacoota | 0.009 (0.008) | 0.009 (0.008) | 0.009 (0.008) | 0.009 (0.008) | 0.009 (0.008) | *0.796 (0.043)* | 0.009 (0.008) | 0.143 (0.044) | 0.010 (0.009) |
| Cape Conran | 0.028 (0.026) | 0.028 (0.026) | 0.028 (0.025) | 0.028 (0.026) | 0.028 (0.025) | 0.088 (0.043) | *0.696 (0.027)* | 0.050 (0.035) | 0.028 (0.026) |
| Tasmania | 0.007 (0.007) | 0.008 (0.007) | 0.007 (0.007) | 0.007 (0.007) | 0.007 (0.007) | 0.256 (0.028) | 0.007 (0.007) | *0.690 (0.022)* | 0.009 (0.009) |
| Tasmania (Ot2) | 0.010 (0.009) | 0.010 (0.009) | 0.010 (0.009) | 0.010 (0.009) | 0.010 (0.009) | 0.013 (0.013) | 0.010 (0.009) | 0.020 (0.015) | *0.910 (0.026)* |

Historical distribution zone: Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden at New South Wales. Range extension zone: Mallacoota, and Cape Conran at Victoria, and north-eastern Tasmania. The common group Ot1 indicated in the text is comprised of individuals from all sites. The distinct group Ot2 is predominately comprised of individuals from Tasmania (red cluster in figures 4.1 and 4.2). Italicised values indicate self-recruitment; values in parentheses indicate standard deviation. Left column indicates where migrants travelled to; top row indicates where migrants originated from

*Genetic diversity*

Allelic richness was high with more than seven alleles at each site; the number of private alleles and heterozygosity in the range extension zone was greater compared to the historical distribution zone, and inbreeding coefficient was significant only for Nambucca Heads, Swansea, and Mallacoota (Table 4.5, Table S4.2, Supporting information). Overall, moderate levels of genetic diversity were observed across sites and loci, and genetic diversity was similar at the range extension compared to the historical distribution zone (Table 4.5).

*Bottleneck analysis*

Overall, no bottleneck effect was detected at the historical distribution or at the range extension zones. However, heterozygosity excess and differences in allele frequencies were identified in both areas, and in each site under the SMM (except for Nambucca Heads and Swansea; Table 4.6).

*Effective population size*

Effective population size at the historical distribution zone was considerably larger (Ne = 1664.6, $P$ = 0.02; Table 4.7) compared to the range extension zone (Ne = 96.1, $P$ = 0.02; Table 4.7). Within the range extension zone the effective population size of the distinct group Ot2 was smaller (Ne = 85.9, $P$ = 0.02; Table 4.7) than the other sites (Mallacoota = 319.4 and Tasmanian component of Ot1 = 316.4, $P$ = 0.02; Table 4.7).

Table 4.5 Descriptive statistics for *Octopus tetricus* along the east coast of Australia

| Zone/Site | N | $N_A$ | $N_{PA}$ | $A_R$ | $H_O$ | $H_E$ | P value | $F_{IS}$ |
|---|---|---|---|---|---|---|---|---|
| Historical distribution | 88 | 14.000 | 2.714 | 13.726 | 0.571 | 0.627 | <0.001 | 0.085 |
| Nambucca Heads | 17 | 7.429 | 0.571 | 7.285 | 0.505 | 0.569 | 0.005 | 0.110* |
| Swansea | 30 | 10.143 | 0.857 | 8.038 | 0.579 | 0.644 | <0.001 | 0.106* |
| Merimbula | 29 | 10.000 | 0.571 | 8.048 | 0.621 | 0.651 | 0.190 | 0.049 |
| Range extension | 91 | 15.143 | 4.429 | 14.604 | 0.628 | 0.688 | <0.001 | 0.084 |
| Mallacoota | 29 | 9.857 | 0.857 | 7.867 | 0.580 | 0.619 | 0.010 | 0.067* |
| Tasmania | 35 | 10.571 | 1.143 | 7.758 | 0.668 | 0.652 | 0.001 | -0.051 |
| Tasmania (Ot2) | 24 | 9.000 | 1.000 | 7.814 | 0.639 | 0.655 | 0.051 | 0.054 |

n, sample size; $N_A$, number of alleles; $N_{PA}$, number of private alleles; $A_R$, allelic richness (standardized to 17 samples); $H_O$, observed heterozygosity; $H_E$, expected heterozygosity; P values for heterozygote deficiency ($P < 0.05$); $F_{IS}$, Inbreeding coefficient. Summary for the historical distribution zone comprises: Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden at New South Wales. Summary for the range extension zone comprises: Mallacoota, and Cape Conran at Victoria, and north-eastern Tasmania. The common group Ot1 indicated in the text is comprised of individuals from all sites. The distinct group Ot2 is predominately comprised of individuals from Tasmania (red cluster in figures 4.1 and 4.2). Asterisk indicates significant $F_{IS}$. Descriptive statistics were not estimated for Ulladulla, Eden and Cape Conran due to their small sample sizes ($n$ <17)

Table 4.6 Output of bottleneck analysis on *Octopus tetricus* along the east coast of Australia

| | Bottleneck tests | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Infinite Allele Model (IAM) | | | Stepwise Mutation Model (SMM) | | | | |
| Zone/Site | I | ii | iii | i | ii | iii | iv | Overall |
| Historical distribution | 0.318 | 0.165 | 0.469 | **0.002** | **<0.001** | 1.000 | No | No |
| Nambucca Heads | 0.349 | 0.220 | 0.766 | 0.108 | **<0.001** | 0.988 | No | No |
| Swansea | 0.593 | 0.339 | 0.406 | 0.100 | **<0.001** | 0.988 | No | No |
| Merimbula | 0.598 | 0.441 | 0.406 | **0.020** | **<0.001** | 0.992 | No | No |
| Range extension | 0.576 | 0.245 | 0.766 | **0.002** | **<0.001** | 1.000 | No | No |
| Mallacoota | 0.586 | 0.094 | 0.656 | **0.021** | **<0.001** | 0.992 | No | No |
| Tasmania | 0.589 | 0.385 | 0.766 | **0.002** | **<0.001** | 1.000 | No | No |
| Tasmania (Ot2) | 0.606 | 0.303 | 0.594 | **0.002** | **<0.001** | 1.000 | No | No |

Summary for the historical distribution zone comprises: Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden at New South Wales. Summary for the range extension zone comprises: Mallacoota, and Cape Conran at Victoria, and north-eastern Tasmania. The common group Ot1 indicated in the text is comprised of individuals from all sites. The distinct group Ot2 is predominately comprised of individuals from Tasmania (red cluster in figures 4.1 and 4.2). For each site, values for sites with ≥17 samples are presented only. i) "sign test" for heterozygosity excess; ii) "standardized differences test" for differences in allele frequencies; iii) "Wilcoxon test" for reduced mean heterozygosity; iv) "mode-shift qualitative test" for distortion of allele frequency distributions. Significance at $P < 0.05$. Possible bottleneck effect is indicated in bold. Yes/No indicates the acceptance/rejection of a possible bottleneck effect

Table 4.7 Effective population size for *Octopus tetricus* along the east coast of Australia

| Zone/Site | Ne | CI (Inferior) | CI (Superior) |
|---|---|---|---|
| Historical distribution | 1664.6 | 243.5 | ∞ |
| Nambucca Heads | 60.2 | 20.6 | ∞ |
| Swansea | ∞ | 128.9 | ∞ |
| Merimbula | 68.5 | 33.7 | 468.8 |
| Range extension | 96.1 | 66.8 | 154.4 |
| Mallacoota | 319.4 | 60.2 | ∞ |
| Tasmania | 316.4 | 70.3 | ∞ |
| Tasmania (Ot2) | 85.9 | 32.4 | ∞ |

Ne, Effective population size; CI, Confidence interval. The common group Ot1 indicated in the text is comprised of individuals from all sites. The distinct group Ot2 is predominately comprised of individuals from Tasmania (red cluster in figures 4.1 and 4.2); $P = 0.02$

**Discussion**

The key findings of this study are that genetic differentiation was detected between sites present within the historical distribution and the range extension zones. A distinct sub-population was identified and was mainly comprised of individuals from north-eastern Tasmania at the range extension zone, although it also contained a few individuals from the historical zone. Migration rates were asymmetrical with greater migration occurring from the historical distribution zone to the range extension zone; where sites at the extension zone had the highest self-recruitment values along the east coast of Australia. The genetic diversity at the range extension zone was

comparable to that detected at the historical distribution area. There was no evidence of bottleneck effects within the historical distribution or range extension zones, but effective population size was relatively small at the range extension zone compared to the historical distribution zone. These features suggest that *O. tetricus* is likely to be able to persist in the range extension zone provided that no demographic effect negatively affects the population.

*Octopus tetricus* individuals clustered into two distinct groups; one group that was common along the east coast of Australia (Ot1) and a distinct group predominately comprised of individuals from Tasmanian waters (Ot2). Phylogenetic analysis demonstrated that individuals belonging to both groups are *O. tetricus*. The presence of the common group Ot1 throughout the historical distribution and the range extension zones is supported by moderate levels of gene flow between sites (low $F_{ST}$ values) and lack of population sub-structure, as well as by shared haplotypes between NSW and Tasmania using mitochondrial DNA (Amor *et al*. 2014). It is likely that the distinct group Ot2 is becoming established in Tasmanian waters from a genotype that is relatively uncommon in the historical distribution zone. However small sample sizes collected along the historical distribution zone may have also led to underestimation of the presence of individuals of the group Ot2 in this zone. The minor migration rates from along mainland Australia support the limited gene flow towards the Tasmanian component of the group Ot2, which assisted the group Ot2 in becoming genetically different to the group Ot1. In addition, the high self-recruitment of the group Ot2, the rapid population turnover and the high reproductive capacity of *O. tetricus* in Tasmanian waters (Ramos *et al.* 2014, 2015) may have further increased the frequency of the distinct genotype in the area. Population differentiation of microbial colonies at the leading edge of range extensions have also been attributed to

a small number of reproducing individuals with fast population turnover (Hallatschek *et al.* 2007). These characteristics provide species high evolutionary capacity (Bromham 2011) and may facilitate their adaptability and long-term persistence in range extension zones (O'Connor *et al.* 2012).

The genetic differentiation in Tasmania between the groups Ot1 and Ot2 seems to occur due to migration rates and self-recruitment rather than because of sampling time, temperature or habitat differentiation. For example, Mallacoota was the main source of migrants towards Tasmania, with greater migration towards the group Ot1 compared to the group Ot2. A greater number of migrants from Mallacoota may have diversified the gene pool in the Tasmanian component of the group Ot1, whereas a limited number of migrants from Mallacoota may have resulted in a lesser diversified gene pool of the Tasmanian component of the group Ot2. In addition, the high levels of self-recruitment and the low migration between the Tasmanian components of Ot1 and Ot2 may have caused the genetic differentiation between both groups.

Contrary to expectations, the levels of genetic diversity and heterozygosity in the distinct group Ot2 were comparable to that of Ot1. These signatures correspond to populations undergoing rapid demographic extension (Excoffier *et al*. 2009); for instance, the rapid range extension of *C. rodgersii* (Banks *et al.* 2010) and *M. roeselii* (Kanuch *et al.* 2014). The sustained genetic diversity in the extension area was facilitated by sufficient gene flow from different source areas along the entire distribution (Roman & Darling 2007) and by the absence of genetic bottleneck along the range extension axis. Sustained genetic diversity may confer high phenotypic plasticity to founder individuals and the ability to respond to natural selection, allowing the population to persist in the extension zone (Dlugosch & Parker 2008;

Kanuch *et al.* 2014). Interestingly, *O. tetricus* appeared to display phenotypic plasticity in Tasmanian waters. The known morphotype for *O. tetricus* consists of long and thin arms, and relatively small mantle in proportion to the rest of the body (Norman *et al.* 2013). However, a distinct morphotype comprising short, thick arms, and a relatively large mantle in proportion to the rest of the body was also present in Tasmanian waters ($n$ = 7 individuals, Ramos *et al.* pers. obs.). Similarly, Amor *et al.* (2014) found discrete morphological differences in male *O. tetricus* between the east coast of mainland Australia and Tasmania. Morphological differences and genetic separation of individuals in Tasmanian waters suggest that the range extension of *O. tetricus* may have occurred before this species was first detected off Tasmania during 2006. Comparative molecular and morphological analyses are necessary to quantify differences of both morphotypes of *O. tetricus*, which may help elucidating when the range extension into Tasmanian waters occurred.

The EAC is presumed to be the main driver of larval transport along the east coast of Australia (Johnson *et al*. 2011; Last *et al.* 2011). Therefore the population structure and connectivity of the *O. tetricus* population is expected to be shaped by the dynamics of the EAC (Ridgway & Dunn 2003; Ridgway 2007; Hill *et al.* 2008). With an assumed planktonic duration of 35–60 days (from closely related *O. vulgaris* reared in the laboratory, Villanueva 1995; Carrasco e*t al*. 2006), paralarvae of *O. tetricus* may be transported the linear distance between Nambucca Heads and Tasmanian waters (~1,150 km) at an average seawater flow of 55 cm $s^{-1}$ (based on Ridgway & Dunn 2003). However, the use of Euclidean distances as a measure of isolation may be a poor predictor of gene flow (White *et al*. 2010), because of the effect of the coastline creating circuitous, turbulent, and nonlinear flow, that joined with eddies and fronts may result in patchy larval dispersal (Siegel *et al*. 2008; Weersing & Toonen

2009; Roughan *et al.* 2011). Still, the dispersion of paralarvae estimated in this study is supported by the connectivity previously detected between the east coast of Australia and Tasmania (Amor *et al.* 2014). *Octopus tetricus* is also likely to disperse across the Tasman Sea, as suggested by the absence of genetic differentiation between the Tasmanian population and its New Zealand counterpart (Amor *et al.* 2014).

To migrate southwards into Tasmanian waters, *O. tetricus* has to pass through a gradient of temperatures between NSW (annual average SST 20.2°C ± 0.2 s.e. at 32°31'15"S and 152°28'45"E) and north-eastern Tamania (annual average SST 15.2°C ± 0.2 s.e. at 39°33'45"S and 148°13'45"E). Sufficient gene flow from along the historical distribution zone, most likely with a different thermal environment, may facilitate adaptation in the range extension zone via the subsequent reproduction of individuals from different source sites (Ibrahim *et al.* 1996; Bridle *et al.* 2010). This may help explain the comparable genetic diversity between the historical distribution and the range extension zones (Verhoeven *et al.* 2010). Maintenance of genetic diversity at sites of the group Ot1 within the range extension at levels concordant with the historical distribution may buffer against any new set of environmental stressors that is different to those present within the historical distribution (Hoffmann & Hercus 2000; Whitney & Gabler 2008; Hoffmann & Sgrò 2011). Maintenance of genetic diversity is therefore likely to contribute to the establishment, early success and persistence of *O. tetricus* in the extension zone (Drake 2006; Roman & Darling 2007). Comparable levels of genetic diversity in range extension areas have also been observed in *C. rodgersii* (Banks *et al.* 2010); whereas the rapid recovery of genetic diversity of *M. roeselii* in new areas was in part attributed to multiple introductions of a large numbers of individuals for long periods of time, as well as due to hybridization of several founding populations (Kanuch *et al.* 2014). These mechanisms seem to

allow recovery of genetic diversity of invasive populations, shedding light on the 'genetic paradox' that has intrigued invasion biologists in recent years (Roman & Darling 2007).

Significant inbreeding values in Nambucca Heads and Swansea suggest that this area is within the trailing edge of the range extension where gene inflow is limited and genetic diversity tends to decrease (Davis & Shaw 2001). In contrast, the negative inbreeding coefficient in Tasmania (Ot1), and high level of heterozygosity, gene flow and migration rate from Mallacoota suggest that Tasmania is within the leading edge of the range extension (Davis & Shaw 2001); these genetic signatures may have a positive impact for the survival of individuals in the range extension area (McInerny *et al*. 2009). However, the accelerated warming along the east coast of Australia is anticipated to shorten the paralarval phase of *O. tetricus*, potentially reducing dispersal capacity, population connectivity (O'Connor *et al*. 2007; Munday *et al*. 2009), and recovery of genetic diversity in the range extension area. Effects of ocean warming on reproductive seasons, frequency of paralarvae releases, swimming capabilities, paralarvae settlement windows, habitat suitability, and paralarvae mortality may also influence the connectivity of populations (Siegel *et al*. 2008). Therefore, incorporation of 'seascape genetics' including oceanographic, life history, and ecological data in the context of ocean warming, into the examination of the population connectivity may provide better understanding of the structure, connectivity, genetic diversity, and capacity of the population of *O. tetricus* to prevail in the new sections of its geographic distribution (Selkoe *et al.* 2010). *Octopus tetricus* has a life-span of 11 months (Ramos *et al.* 2014) and allele frequencies could change between years of collection. Future research should therefore include samples from consecutive years within sites to assess stability of allele frequencies through time.

Additionally, the robustness of our conclusions could be strengthened by using larger sample sizes in any future analyses.

These findings suggest that gene flow from different areas along the historical distribution of *O. tetricus* is crucial in maintaining the genetic diversity of the population in the range extension zone, and increasing its adaptive capacity and persistence. However, demographic and environmental stochasticity could have negative impacts on the growth and persistence of the population given the small effective population size (Ne <100) in some sites, i.e. Nambucca Heads, Merimbula, and the Tasmanian component of the Ot2 group (Hoffmann & Sgrò 2011). Still, the effective population size of those sites may be sufficient to limit loss in total fitness to ≤ 10% and avoid inbreeding depression (Frankham *et al.* 2014). The larger the effective population size, the less likely that genetic drift or inbreeding depression will reduce the capacity of the founders to adapt locally (Sexton *et al*. 2009). Therefore, to increase genetic diversity and avoid extinction risk, the founder population may depend on the gene flow from along the historical distribution, where the effective population size is large enough (Ne > 1000) to maintain evolutionary potential (Gomulkiewicz *et al*. 1999; Holt 2003; Frankham *et al.* 2014; Signorile *et al*. 2014). In summary the genetic signatures at the leading edge of the range extension were lesser genetic differentiation from the rest of the population, lesser self-recruitment and inbreeding, greater immigration and gene flow from source sites, and greater effective population size and genetic diversity in the Tasmanian component of group Ot1 compared to the Tasmanian component of group Ot2. Finally, two mechanisms may allow *O. tetricus* to prevail in the range extension zone: 1) high and constant levels of gene flow from a wide variety of source areas to maintain genetic diversity of the Tasmanian component of the group Ot1; and 2) occasional but sufficient gene flow

towards the highly self-recruited Tasmanian component of the group Ot2 that already has sufficient genetic diversity.

This study suggests that the range extension zone of *O. tetricus* is genetically diverse, with a distinct predominately Tasmanian sub-population. High gene flow from a diversity of source areas along the entire distribution seems to play an important role by promoting relatively high genetic diversity and counteracting bottleneck effects at extension areas, although demographic or environmental stochasticity is likely to influence this range extension given the small effective population sizes detected in some sites. The genetic signatures examined in this study suggest that *O. tetricus* is well placed to be able to persist in its range extension zone provided that no demographic effect negatively affects the population.

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# Chapter 5

## General discussion

## Chapter 5. General discussion

Most of our knowledge on the factors contributing to changes in distribution is based on the invasion ecology framework (e.g. McMahon 2002; Whitney & Gabler 2008; Phillips 2009; Phillips *et al.* 2010). However, this study has provided important insights on how life history characteristics and population dynamics relate to the range extension of a marine species, *Octopus tetricus*. The common Sydney octopus, *O. tetricus*, recently has undertaken a range extension southwards along the east coast of Australia, likely associated to the strengthening of the East Australian Current (EAC) that is in part causing the accelerated warming of south-eastern Australian waters. In Tasmanian waters, *Octopus tetricus* had a relatively small body size, fast growth rates, and rapid population turnover (Chapter 2). Moreover, individuals were reproductively viable, with high reproductive potential, and the reproductive cycle was timed with favourable environmental conditions (Chapter 3). Examination of population genetics revealed that the population was sub-structured, with a group that was common along the east coasts of mainland Australia and Tasmania, and with a distinct group predominately comprised of individuals from Tasmanian waters. In contrast to expectations, genetic diversity was maintained at the range extension area compared to the historical distribution area, probably caused by moderate migration rates from different sites along the entire distribution. The gene flow from a diversity of habitats and environments, and relatively high genetic diversity along the range extension axis may maintain the adaptive capacity of this species in the range extension area (Chapter 4). Overall, these findings suggest that the life history characteristics and population dynamics of *O. tetricus* may facilitate the establishment and prevalence of the population in the new sections of its geographic distribution (Fig. 5.1).

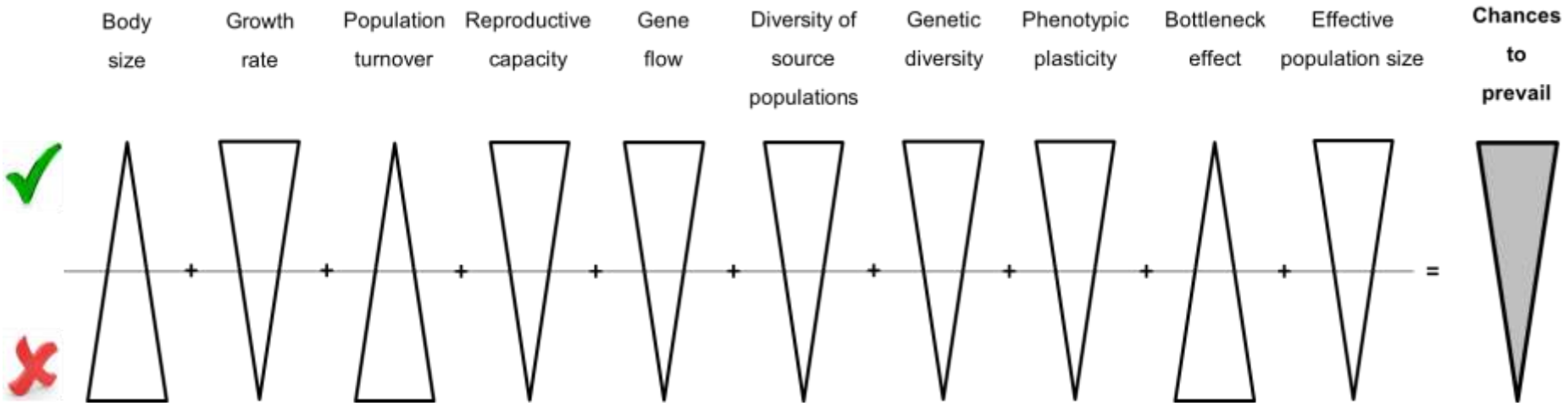


Figure 5.1 Factors examined in this study that influence the range extension of *Octopus tetricus*, likely associated to oceanic warming. The white triangles indicate the magnitude or level of each factor, where the wide side of the triangle indicates greater magnitude or level and the narrow side of the triangle indicates lesser magnitude or level. Factors above the grey line are positive to establish and prevail in new sections of the geographic distribution

While it was not possible to compare life history characteristics of *O. tetricus* in the range extension zone with those in the historical distribution zone, this study suggests that the component of the population of *O. tetricus* in Tasmanian waters was characterized by an r-life history strategy. Colonist populations of invasive species such as aquatic invertebrates, amphibians, and fishes also exhibit r-selected traits that provide an adaptive strategy for fast population increase and establishment in new areas (McMahon 2002; Phillips 2009; Amundsen *et al.* 2012). Likewise, range-shifting species of invertebrates and fishes along south-eastern Australia have life history characteristics and migration capacity comparable to *O. tetricus*. These range-shifting species have high fecundity, great dispersal capacity, little reliability on habitat or prey, and large latitudinal range (for some examples see Table 5.1).

Range shifting species of fishes have faster life cycles and smaller body sizes than species that do not undertake range shifts (Perry *et al*. 2005). An explanation is that fishes of small body have fast rates of intrinsic population growth (Denney *et al.* 2002) and therefore are expected to undertake faster range extensions. Interestingly, invertebrates of large body size have also shown great rates of range extension (Roy *et al.* 2001). The fast growth rates of *O. tetricus* in Tasmanian waters resulted in individuals that reached maturity early in their life. As a consequence, those individuals had a short life span that may facilitate a rapid turnover of the population in the range extension area. The rapid turnover of the population may benefit its range extension because selection acts on biological traits every generation (Lee 2002); genotypes that may be suitable for the new environments are thus likely to be selected more often in species with shorter generation times in comparison with long-lived species (Berteaux *et al*. 2004; Hoffmann & Willi 2008). *Octopus tetricus* may thus be able to adapt rapidly to the changing environment in new areas (Lee 2002).

Table 5.1 Characteristics of range shifting species along south-eastern Australia

| Common name (Species) | Body size | Growth rate | Life span | Fecundity | Age at maturity | Capacity for larval dispersal | Capacity for active migration | Generalist vs specialist | Physiological tolerance |
|---|---|---|---|---|---|---|---|---|---|
| Common Sydney octopus (*Octopus tetricus*) | Small[1] (2.3 kg total weight) | Fast[1] (0.014 day$^{-1}$) | Short[1] (<1 year) | High[2] (~280,000 eggs spawning$^{-1}$) | Early[2] (224 days) | Medium-High*[3,4] (35-60 days) | Unknown | Generalist[5] (rocky reefs, sandy bottom; carnivore) | High[1,2] (Queensland to Tasmania) |
| Firebrick seastar (*Asterodiscides truncatus*) | Small[6] (17-cm radius) | Slow*[7] (10 mm year$^{-1}$) | Unknown | High*[8] (~160,000 eggs spawning$^{-1}$) | Unknown | Medium-High*[9] (40-70 days) | Low | Medium[10] (reef; omnivorous) | Low[10] (northern NSW to Tasmania) |
| Longspine sea urchin (*Centrostephanus rodgersii*) | Small[11] (13-cm total diameter) | Slow[12] (10–24 mm year$^{-1}$) | Unknown | High[11] | Medium[13] (<3 years old) | High[14] (100 days) | Low[15] (≤600m$^{-2}$) | Generalist[16,17] (reef, rocky habitat; herbivorous) | Low[18] (northern NSW to Tasmania) |
| Eastern king prawn (*Melicertus plebejus*) | Small[19] (6-cm carapace length) | Fast[20] | Medium[21] (~10 years) | High*[22] (100,000–650,000 eggs spawning$^{-1}$) | Medium[21] (2–10 years) | High[23] (>60 days) | High[20,21] (≤1200 km) | Medium[21] (estuarine, neritic; carnivore) | High[24] (northern Queensland to Tasmania) |
| Yellowtail kingfish (*Seriola lalandi*) | Large[25] (2.5 m) | Slow[26] (0.5–1.23 mass gain day$^{-1}$) | Medium[25] (12 years) | High[27] (4 million eggs spawning$^{-1}$) | Medium[25] (5–7years) | Medium[27] (35 days) | High[28] (≤3000 km) | Generalist[25] (pelagic; carnivore) | High[25] (Queensland to Tasmania) |

Life span: short (<1 year), medium (1–20 years), long (>20 years); Fecundity: low (<100 eggs year$^{-1}$), medium (100–20,000 eggs year$^{-1}$), high (>20,000 eggs year$^{-1}$); Age at maturity: early (<1 year), medium (1–3 years), late (>3 years); Capacity for larval dispersal: low (<2 weeks or no larval dispersal), medium (2–8 weeks), high (2 months); Capacity for active migration: low (<10 km), medium (10–1000 km), high (>1000 km);

Reliance on habitat or prey: specialist (reliance on habitat and prey), medium (reliance on one, habitat or prey), generalist (no reliance on habitat nor prey); Physiological tolerance (latitudinal range of distribution as a proxy of environmental tolerance): low (<10° latitude), medium (10–20° latitude), high (>20° latitude); * Characteristics that are unknown for the species of interest but that were assumed from other species of the same or close taxonomic group. [1]Ramos *et al.* (2014); [2]Ramos *et al.* (2015); [3]Villanueva (1995); [4]Carrasco *et al.* (2006); [5]Scheel *et al.* (2014); [6]Rowe (1997); [7]Laptikhovsky *et al.* (2015); [8]Grange *et al.* (2004); [9]Sunday *et al.* (2014); [10]http://australianmuseum.net.au/asterodiscides-truncatus [accessed 25 May 2015]; [11]Ling *et al.* (2008); [12]Pecorino *et al.* (2012); [13]King *et al.* (1994); [14]Huggett *et al.* (2005); [15]Ling *et al.* (2009); [16]http://bie.ala.org.au/species/Centrostephanus+rodgersii [accessed 25 May 2015]; [17]Perkins *et al.* (2015); [18]Pecorino (2012); [19]Bracini *et al.* (2013); [20]Lloyd-Jones *et al.* (2012); [21]Montgomery (2011); [22]Penn (1980); [23]Montgomery *et al.* (2007); [24]http://bie.ala.org.au/species/Melicertus+plebejus [accessed 25 May 2015]; [25]Bray (2011); [26]Moran *et al.* (2009); [27]Stuart & Drawbridge (2013); [28]Gillanders *et al.* (2001)

*Octopus tetricus* also appeared to fulfil most of the requirements of successful reproduction at the range extension area. For instance, brooding females were observed and fecundity was high and comparable to that of closely related species within their core distributions (e.g. *O. vulgaris*: Silva *et al.* 2002; Otero *et al.* 2007). The high fecundity of *O. tetricus* may be an advantage over native species of octopus in the same area that have a lower fecundity (Travis & Dytham 2002), e.g. *O. pallidus* (Leporati *et al.* 2008a). In a similar way that selection may act frequently on *O. tetricus* as a function of its rapid population turnover, selection may also act more often on its offspring as a function of its high fecundity. For instance, the genome is copied more often as the number of offspring produced increases, which may result in greater frequency of genotypes suitable for the new environments (Bromham 2011). In addition, eggs of *O. tetricus* developed successfully in the cool temperatures of Tasmanian waters. Furthermore, the synchronization of reproduction events of *O. tetricus* with favourable environmental conditions in Tasmanian waters may promote paralarval survival and recruitment, and facilitate opportunities for the population to optimize resources within the range extension area. Similar synchronies of reproductive events and favourable environmental conditions have been reported for other species of octopus and squids, which in turn may affect reproduction, growth rates, life span (Forsythe and Hanlon 1988; Pecl 2004; Pecl *et al*. 2004), and potentially abundance of individuals (Kang *et al*. 2002; Otero *et al*. 2008). Overall, Chapters 2 and 3 of this study suggest that the life history characteristics of *O. tetricus* in Tasmanian waters may facilitate its capacity to rapidly increase the size of the emerging population. With rapid population growth, the emerging population may also increase its capacity to establish and prevail in the new sections of its geographic distribution, providing there is survival of offspring in the new habitats.

The capacity of the population of *O. tetricus* to establish and prevail in the range extension area is likely influenced by the connectivity of the population along its entire distribution in Australian waters, including the range extension zone. Population connectivity may have allowed the levels of genetic diversity to be comparable between the historical distribution and the range extension zones, which is essential to sustain the adaptive potential and persistence of the population in the range extension zone (Etterson & Shaw 2001). Connectivity of the population of *O. tetricus* via the dispersion of the planktonic paralarvae phase was likely influenced by the dynamics of the EAC. Similarly, the EAC seems to be associated with the range extension of many other marine species in the region, e.g. from invertebrates to fishes (Johnson *et al*. 2011; Last *et al*. 2011). With a planktonic paralarval phase that may last up to two months, the high capacity for dispersal of *O. tetricus* during its planktonic phase may allow sufficient levels of gene flow along its entire geographic distribution in Australian waters. This is further supported by the asymmetric gene flow that was predominantly sourced from along the historical distribution zone towards the range extension area. The analysis of migration rates suggests that paralarvae were sourced from different sites along the historical distribution, likely exposed to different environmental conditions. If paralarvae from different environmental conditions subsequently settle and reproduce in the range extension area, genetic diversity may increase and potentially create new genotypes or traits that may positively affect the persistence of the population in the new sections of the geographic distribution (Verhoeven *et al*. 2010). Overall, Chapter 4 suggests that continuous gene flow from different source areas, and the likely subsequent reproduction between those individuals sourced from different sites and that settle in the range extension area, play a crucial role to maintain genetic diversity and adaptive

potential of the population of *O. tetricus* at the new sections of its geographic distribution. This finding is in agreement with genetic diversity not being reduced along the extension axis of other range extender populations, i.e. *Centrostephanus rodgersii* (Banks *et al*. 2010) and *Metriptera roeselii* (Kanuch *et al*. 2014). Furthermore, this study provides supporting evidence where continuous gene flow from a wide diversity of source areas may allow range shifting populations to overcome the negative impacts of low genetic diversity, the so called 'genetic paradox' (Roman & Darling 2007).

In summary, fast growth rates, short life span and therefore rapid population turnover, high fecundity, viability of embryos, high gene flow, high diversity of source populations, high genetic diversity, and the absence of bottleneck or negative demographic effects seemed to be the main factors that favour the range extension of *O. tetricus* by facilitating the establishment and prevalence of the population in the new sections of its geographic distribution (Fig. 5.1). However, many other factors that were not examined in this study may also be relevant to the range extension process of *O. tetricus*, e.g. thermal physiology, the likely reduction of the paralarval phase due to the continuing ocean warming (O'Connor *et al*. 2007; Munday *et al*. 2009), which may negatively affect the population connectivity of *O. tetricus*, the oceanographic features that influence the dispersion of paralarvae, the inter-specific and intra-specific interactions in the range extension area, and the complexity of the community at the range extension area, among others. Therefore, it is important that further studies consider the relevance and magnitude of these factors and their interactions.

Further studies should examine the life history characteristics and population dynamics of *O.tetricus* within the historical distribution and at the range extension

areas. This will allow the comparison of such characteristics between the core geographic distribution and the range extension areas, and determine if there is a detrimental effect on the performance of *O. tetricus* at the new sections of its geographic distribution.

It is expected that the duration of the planktonic parlarval phase of *O. tetricus* is reduced with ocean warming, which subsequently may affect the connectivity of the population (O'Connor *et al*. 2007; Munday *et al*. 2009). Examination of the genetic connectivity of the population of *O. tetricus* by the incorporation of 'seascape genetics' including oceanographic features (e.g. currents, eddies, fronts, coasts, etc.), as well as life history characteristics and other biological factors (e.g. duration of reproductive seasons, paralarval duration, paralarval settlement windows, scale and frequency of paralarval releases, dispersal capacity, paralarval mortality, and habitat suitability) may provide better understanding of the connectivity, structure, and capacity of the population of *O. tetricus* to prevail longer-term in the new sections of its geographic distribution.

Species with larger latitudinal ranges occupy a greater proportion of their potential thermal niches, and seem to undertake the greatest range shifts as they are best able to track isotherms (Sunday *et al.* 2015). Therefore, thermal windows should be examined at the historical distribution and at the range extension areas, as well as under projections of ocean warming. For example, further studies could examine the effect of temperature on embryonic development, and on the aerobic scope and behaviour of paralarvae, juveniles, non-mature adults, and mature adults (Pörtner & Farrell 2008; Higgins *et al*. 2012). This information is important to foresee the performance of *O. tetricus* in growth and reproduction, among others under current and future ocean warming scenarios. The physical environment and the inter-specific

and intra-specific interactions are also likely to affect the performance and establishment of *O. tetricus* in new sections of its geographic distribution (Colautti *et al.* 2006). Therefore, the habitat and structure of the marine community at the range extension area should be characterised.

The phenotypic plasticity of *O. tetricus* could be examined with morphological and population genetic approaches along the east coast of Australia, including Tasmanian waters. In addition, mutation rates could be studied in relation to life span and reproductive potential, which may allow estimating the rate of favourable and negative mutations, or genetic traits that are created every generation and every batch of offspring (Bromham 2011). Knowledge on phenotypic plasticity, mutation rates, and the nature of the mutations may shed light on the adaptive capacity of *O. tetricus* to new environments.

Invertebrates at higher trophic levels (i.e. predators) seem to extend their ranges faster (Sunday *et al.* 2015). The range extension of *O. tetricus* may thus cause changes in the structure of the community and in the function of the ecosystem at the range extension area. In turn this could impact commercial fisheries, for example by predation of *O. tetricus* on local species of commercial interest. Hence it is important to characterize the diversity of species predated upon by *O. tetricus* in order to anticipate the potential ecological and economic impacts that this species may lead to within the extension areas.

Knowledge on population size, recruitment, and mortality may allow estimation of the growth of the population in the range extension area. In addition, implementation of species distribution models incorporating physiological limits, phenotypic plasticity, and adaptive evolution may allow prediction of the distribution of *O. tetricus* under current and projected ocean warming. This information is

essential to elucidate the colonization capacity of *O. tetricus* under current and projected ocean warming scenarios.

This study on the range extension of *O. tetricus* will underpin many of the suggested research areas above to develop a more complete understanding of the factors that influence the arrival, establishment, spread, and prevalence of range extending species in new sections of their geographic distribution. These types of studies are necessary to predict the winners and losers in the face of ocean warming, as the number of range shifting species is expected to increase in response to accelerated ocean warming (Parmesan & Yohe 2003; Sunday *et al*. 2012; Pinsky *et al*. 2013). The information generated by these studies may thus help us to anticipate the potential ecological and socio-economic impacts that these range shifts may cause (Madin *et al.* 2012).

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**Supporting information**

Table S2.1 Determination of sex and maturity for *Octopus tetricus* based on the macroscopic characteristics of the gonads. Adapted from Mangold (1983b) and Dia (1988)

| Maturity stage | Female | Male |
|---|---|---|
| Immature | Whitish ovary. Small oviducal glands that are white, or orange at the base. Oviducal glands are located midway down or further up in the narrow oviducts | Accessory gland systems and testis are whitish and indistinct, or the testis is larger than the accessory gland and visible through the wall of the genital bag. Few spermatophores are present in the spermatophoric organ |
| Mature | Ovary large and yellow or orange, packed tightly with eggs that might be also present in the oviduct. Oviducal glands are large, dark in colour and positioned at the proximal oviduct; oviducts are longer and thick | Testis and accessory gland are of similar size. Spermatophores are present Needham's sac; spermatophores can also be present in the penis |
| Spent | Shrunken purple ovary only with follicles and a few fully formed eggs. Oviducal glands are larger and pale, and the oviducts are flaccid | Testis is small and striated; few spermatophores still present in the penis and/or Needham's sac |

Table S2.2 Akaike Information Criterion (AIC) and Akaike weight (wAIC) for each growth model fitted to mantle weight at age for *Octopus tetricus* that hatched in warm or cool seasons. Individuals were collected at north-eastern Tasmania, Australia during 2011

| | Warm | | Cool | |
|---|---|---|---|---|
| Growth model | AIC | wAIC | AIC | wAIC |
| Gompertz | -3129.39 | 1 | -13709.12 | 1 |
| Exponential | -2615.98 | <0.0001 | -9572.86 | 0 |
| Power | 787.16 | 0 | 1229.35 | 0 |
| Linear | 784.14 | 0 | 1219.75 | 0 |

Table S3.1 Oocyte morphological groups (based on Laptikhovsky & Nigmatullin 1992) and their correspondence with the phases of oocyte development (Burukovsky *et al*. 1977) found in females of *Octopus tetricus* from north-eastern Tasmania, Australia, during 2011

| Oocyte group | Oocyte external morphology | Oocyte developmental stage |
|---|---|---|
| 1 | Small and polygonial shape, transparent | Second phase of previtellogenesis (PV), primary follicle |
| 2 | Oval or globate shaped, transparent | Third phase of PV, simple follicle |
| 3 | Leaf-like shape with numerous shallow longitudinal grooves in the surface, dark colour | Phases of complicated follicle. Formation of follicular folds, preparing for vitellogenesis (VG) |
| 4 | Nearly spherical shape, covered with reticulate grooves, dark colour | First and second phases of VG, vacuolization and yolk accumulation |
| 5 | Rounded, reticulate grooves almost disappeared but persistent around the vegetative pole, yellow colour | Third phase of VG, expulsion of follicle folds |
| 6 | Oval with smooth surface, amber-yellow colour | Fourth phase of VG, ovulated ripe egg |

Table S4.1 Probability for linkage disequilibrium ($P < 0.05$) for loci comparison across individuals of *Octopus tetricus* along the east coast of Australia

| Site | Locus 1 | Locus 2 | P value | s.e. | Switches |
|---|---|---|---|---|---|
| Nambucca Heads | Ovul01 | Ovul02 | 1.000 | 0.000 | 11640 |
| Nambucca Heads | Ovul01 | Ovul05 | 0.374 | 0.002 | 72281 |
| Nambucca Heads | Ovul02 | Ovul05 | 0.874 | 0.002 | 62578 |
| Nambucca Heads | Ovul01 | Ovul08 | 0.324 | 0.005 | 60656 |
| Nambucca Heads | Ovul02 | Ovul08 | 0.498 | 0.007 | 42341 |
| Nambucca Heads | Ovul05 | Ovul08 | 0.124 | 0.001 | 82756 |
| Nambucca Heads | Ovul01 | Ovul09 | 1.000 | 0.000 | 14480 |
| Nambucca Heads | Ovul02 | Ovul09 | 1.000 | 0.000 | 7062 |
| Nambucca Heads | Ovul05 | Ovul09 | 0.685 | 0.004 | 63326 |
| Nambucca Heads | Ovul08 | Ovul09 | 0.306 | 0.008 | 48229 |
| Nambucca Heads | Ovul01 | Ovul14 | 1.000 | 0.000 | 15025 |
| Nambucca Heads | Ovul02 | Ovul14 | 1.000 | 0.000 | 6926 |
| Nambucca Heads | Ovul05 | Ovul14 | 1.000 | 0.000 | 65015 |
| Nambucca Heads | Ovul08 | Ovul14 | 0.735 | 0.005 | 49600 |
| Nambucca Heads | Ovul09 | Ovul14 | 1.000 | 0.000 | 9053 |
| Nambucca Heads | Ovul01 | Ovul16 | 0.059 | 0.001 | 186825 |
| Nambucca Heads | Ovul02 | Ovul16 | 0.689 | 0.003 | 154160 |
| Nambucca Heads | Ovul05 | Ovul16 | 0.188 | 0.001 | 187854 |
| Nambucca Heads | Ovul08 | Ovul16 | 0.387 | 0.002 | 220102 |
| Nambucca Heads | Ovul09 | Ovul16 | 0.872 | 0.002 | 166887 |
| Nambucca Heads | Ovul14 | Ovul16 | 0.953 | 0.001 | 163576 |
| Swansea | Ovul01 | Ovul02 | 0.134 | 0.014 | 9898 |

| | | | | | |
|---|---|---|---|---|---|
| Swansea | Ovul01 | Ovul05 | 0.062 | 0.004 | 28708 |
| Swansea | Ovul02 | Ovul05 | 1.000 | 0.000 | 9513 |
| Swansea | Ovul01 | Ovul08 | 0.999 | 0.000 | 66992 |
| Swansea | Ovul02 | Ovul08 | 0.196 | 0.009 | 28255 |
| Swansea | Ovul05 | Ovul08 | 0.856 | 0.005 | 43638 |
| Swansea | Ovul01 | Ovul09 | 0.506 | 0.016 | 12888 |
| Swansea | Ovul02 | Ovul09 | 1.000 | 0.000 | 1825 |
| Swansea | Ovul05 | Ovul09 | 0.819 | 0.013 | 10538 |
| Swansea | Ovul08 | Ovul09 | 0.970 | 0.003 | 31095 |
| Swansea | Ovul01 | Ovul14 | 0.896 | 0.007 | 24701 |
| Swansea | Ovul02 | Ovul14 | 1.000 | 0.000 | 5038 |
| Swansea | Ovul05 | Ovul14 | 0.593 | 0.012 | 16932 |
| Swansea | Ovul08 | Ovul14 | 0.690 | 0.008 | 47579 |
| Swansea | Ovul09 | Ovul14 | 1.000 | 0.000 | 6091 |
| Swansea | Ovul01 | Ovul16 | 0.581 | 0.008 | 49509 |
| Swansea | Ovul02 | Ovul16 | 0.646 | 0.014 | 21265 |
| Swansea | Ovul05 | Ovul16 | 0.074 | 0.005 | 34400 |
| Swansea | Ovul08 | Ovul16 | 0.299 | 0.006 | 75690 |
| Swansea | Ovul09 | Ovul16 | 0.667 | 0.012 | 23733 |
| Swansea | Ovul14 | Ovul16 | 0.412 | 0.010 | 36998 |
| Ulladulla | Ovul01 | Ovul02 | 0.101 | 0.001 | 366229 |
| Ulladulla | Ovul01 | Ovul08 | 0.099 | 0.001 | 399285 |
| Ulladulla | Ovul02 | Ovul08 | 0.100 | 0.001 | 366791 |
| Ulladulla | Ovul01 | Ovul09 | 0.099 | 0.000 | 399847 |
| Ulladulla | Ovul02 | Ovul09 | 0.100 | 0.001 | 366994 |

| | | | | | |
|---|---|---|---|---|---|
| Ulladulla | Ovul08 | Ovul09 | 0.100 | 0.001 | 399491 |
| Ulladulla | Ovul01 | Ovul14 | 0.200 | 0.001 | 333197 |
| Ulladulla | Ovul02 | Ovul14 | 0.600 | 0.002 | 199475 |
| Ulladulla | Ovul08 | Ovul14 | 0.200 | 0.001 | 333442 |
| Ulladulla | Ovul09 | Ovul14 | 0.199 | 0.001 | 332848 |
| Merimbula | Ovul01 | Ovul02 | 0.460 | 0.023 | 12549 |
| Merimbula | Ovul01 | Ovul05 | 0.224 | 0.008 | 45531 |
| Merimbula | Ovul02 | Ovul05 | 0.202 | 0.018 | 15565 |
| Merimbula | Ovul01 | Ovul08 | 0.525 | 0.007 | 57052 |
| Merimbula | Ovul02 | Ovul08 | 0.771 | 0.012 | 21045 |
| Merimbula | Ovul05 | Ovul08 | 0.087 | 0.004 | 54086 |
| Merimbula | Ovul01 | Ovul09 | 0.247 | 0.016 | 15059 |
| Merimbula | Ovul02 | Ovul09 | 1.000 | 0.000 | 2112 |
| Merimbula | Ovul05 | Ovul09 | 0.154 | 0.012 | 18046 |
| Merimbula | Ovul08 | Ovul09 | 0.751 | 0.010 | 23472 |
| Merimbula | Ovul01 | Ovul14 | 0.397 | 0.011 | 34649 |
| Merimbula | Ovul02 | Ovul14 | 1.000 | 0.000 | 6789 |
| Merimbula | Ovul05 | Ovul14 | 0.253 | 0.008 | 34853 |
| Merimbula | Ovul08 | Ovul14 | 0.788 | 0.007 | 43623 |
| Merimbula | Ovul09 | Ovul14 | 0.350 | 0.024 | 8175 |
| Merimbula | Ovul01 | Ovul16 | 0.728 | 0.007 | 57252 |
| Merimbula | Ovul02 | Ovul16 | 0.754 | 0.013 | 22294 |
| Merimbula | Ovul05 | Ovul16 | 0.514 | 0.008 | 54069 |
| Merimbula | Ovul08 | Ovul16 | 0.770 | 0.005 | 65285 |
| Merimbula | Ovul09 | Ovul16 | 0.721 | 0.011 | 24417 |

| | | | | | |
|---|---|---|---|---|---|
| Merimbula | Ovul14 | Ovul16 | 0.727 | 0.008 | 44835 |
| Eden | Ovul01 | Ovul02 | 1.000 | 0.000 | 51803 |
| Eden | Ovul01 | Ovul05 | 0.178 | 0.002 | 139650 |
| Eden | Ovul02 | Ovul05 | 1.000 | 0.000 | 109703 |
| Eden | Ovul01 | Ovul08 | 1.000 | 0.000 | 239103 |
| Eden | Ovul02 | Ovul08 | 0.572 | 0.002 | 213790 |
| Eden | Ovul05 | Ovul08 | 1.000 | 0.000 | 308909 |
| Eden | Ovul01 | Ovul09 | 1.000 | 0.000 | 51483 |
| Eden | Ovul02 | Ovul09 | 1.000 | 0.000 | 28983 |
| Eden | Ovul05 | Ovul09 | 0.400 | 0.003 | 110031 |
| Eden | Ovul08 | Ovul09 | 1.000 | 0.000 | 214195 |
| Eden | Ovul01 | Ovul14 | 1.000 | 0.000 | 64570 |
| Eden | Ovul02 | Ovul14 | 1.000 | 0.000 | 38321 |
| Eden | Ovul05 | Ovul14 | 0.666 | 0.003 | 124611 |
| Eden | Ovul08 | Ovul14 | 0.856 | 0.001 | 223071 |
| Eden | Ovul09 | Ovul14 | 1.000 | 0.000 | 38123 |
| Eden | Ovul01 | Ovul16 | 1.000 | 0.000 | 70225 |
| Eden | Ovul02 | Ovul16 | 0.207 | 0.005 | 46586 |
| Eden | Ovul05 | Ovul16 | 1.000 | 0.000 | 124754 |
| Eden | Ovul08 | Ovul16 | 0.215 | 0.002 | 228933 |
| Eden | Ovul09 | Ovul16 | 1.000 | 0.000 | 46149 |
| Eden | Ovul14 | Ovul16 | 1.000 | 0.000 | 57132 |
| Mallacoota | Ovul01 | Ovul02 | 0.307 | 0.022 | 10202 |
| Mallacoota | Ovul01 | Ovul05 | 0.082 | 0.006 | 27580 |
| Mallacoota | Ovul02 | Ovul05 | 0.775 | 0.016 | 11808 |

| | | | | | |
|---|---|---|---|---|---|
| Mallacoota | Ovul01 | Ovul08 | 0.978 | 0.002 | 45494 |
| Mallacoota | Ovul02 | Ovul08 | 0.689 | 0.013 | 19747 |
| Mallacoota | Ovul05 | Ovul08 | 0.415 | 0.009 | 37010 |
| Mallacoota | Ovul01 | Ovul09 | 0.709 | 0.016 | 14058 |
| Mallacoota | Ovul02 | Ovul09 | 0.050 | 0.017 | 2410 |
| Mallacoota | Ovul05 | Ovul09 | 0.227 | 0.012 | 14303 |
| Mallacoota | Ovul08 | Ovul09 | 0.335 | 0.011 | 24051 |
| Mallacoota | Ovul01 | Ovul14 | 0.558 | 0.015 | 24669 |
| Mallacoota | Ovul02 | Ovul14 | 0.174 | 0.024 | 6141 |
| Mallacoota | Ovul05 | Ovul14 | 0.376 | 0.015 | 21054 |
| Mallacoota | Ovul08 | Ovul14 | 0.844 | 0.009 | 34876 |
| Mallacoota | Ovul09 | Ovul14 | **0.020** | 0.005 | 8872 |
| Mallacoota | Ovul01 | Ovul16 | 0.515 | 0.010 | 48976 |
| Mallacoota | Ovul02 | Ovul16 | 0.109 | 0.008 | 23544 |
| Mallacoota | Ovul05 | Ovul16 | 0.842 | 0.005 | 40387 |
| Mallacoota | Ovul08 | Ovul16 | 0.901 | 0.003 | 59370 |
| Mallacoota | Ovul09 | Ovul16 | 0.968 | 0.003 | 27871 |
| Mallacoota | Ovul14 | Ovul16 | **0.045** | 0.004 | 39190 |
| Tasmania | Ovul01 | Ovul02 | 0.371 | 0.036 | 3286 |
| Tasmania | Ovul01 | Ovul05 | **0.000** | 0.000 | 26377 |
| Tasmania | Ovul02 | Ovul05 | 0.412 | 0.030 | 8773 |
| Tasmania | Ovul01 | Ovul08 | 0.133 | 0.009 | 35595 |
| Tasmania | Ovul02 | Ovul08 | 0.850 | 0.014 | 17995 |
| Tasmania | Ovul05 | Ovul08 | 0.280 | 0.008 | 60602 |
| Tasmania | Ovul01 | Ovul09 | 0.649 | 0.033 | 5633 |

| | | | | | |
|---|---|---|---|---|---|
| Tasmania | Ovul02 | Ovul09 | 1.000 | 0.000 | 1059 |
| Tasmania | Ovul05 | Ovul09 | 0.681 | 0.018 | 17669 |
| Tasmania | Ovul08 | Ovul09 | 0.173 | 0.012 | 28874 |
| Tasmania | Ovul01 | Ovul14 | 0.076 | 0.012 | 11023 |
| Tasmania | Ovul02 | Ovul14 | 0.178 | 0.028 | 3117 |
| Tasmania | Ovul05 | Ovul14 | 0.805 | 0.014 | 25039 |
| Tasmania | Ovul08 | Ovul14 | 0.055 | 0.005 | 36990 |
| Tasmania | Ovul09 | Ovul14 | 1.000 | 0.000 | 4943 |
| Tasmania | Ovul01 | Ovul16 | 0.214 | 0.013 | 28618 |
| Tasmania | Ovul02 | Ovul16 | 0.684 | 0.021 | 13116 |
| Tasmania | Ovul05 | Ovul16 | **0.048** | 0.004 | 42771 |
| Tasmania | Ovul08 | Ovul16 | 0.218 | 0.007 | 50530 |
| Tasmania | Ovul09 | Ovul16 | 0.515 | 0.012 | 42933 |
| Tasmania | Ovul14 | Ovul16 | 0.275 | 0.012 | 31613 |

Historical distribution zone: Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden at New South Wales. Range extension zone: Mallacoota, and Cape Conran at Victoria, and north-eastern Tasmania. Loci comparisons in linkage disequilibrium are indicated in bold. s.e., standard error

Table S4.2 Genetic variability at seven microsatellite loci within collection sites, and historical distribution and range extension zones for *Octopus tetricus* along the east coast of Australia

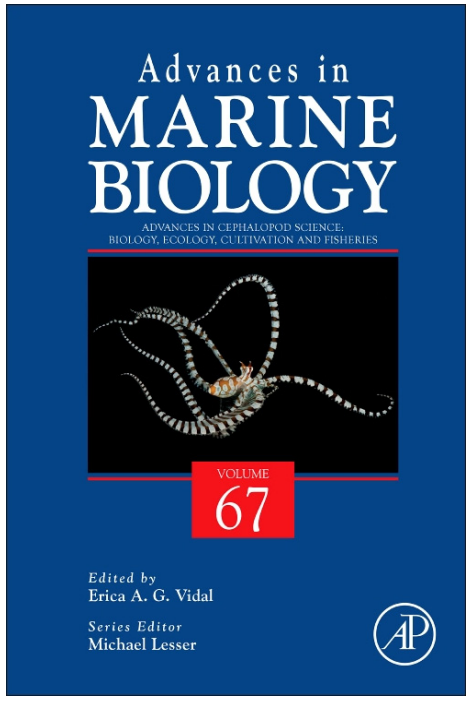
| Site/Zone | n | $N_A$ | $N_{PA}$ | $A_R$ | $H_O$ | $H_E$ | $F_{IS}$ | P value |
|---|---|---|---|---|---|---|---|---|
| Ovul01 | | | | | | | | |
| Nambucca Heads | 16 | 7 | 2 | 7.000 | 0.750 | 0.760 | 0.014 | 0.546 |
| Swansea | 29 | 8 | 1 | 6.171 | 0.724 | 0.731 | 0.010 | 0.173 |
| Merimbula | 29 | 7 | 0 | 6.181 | 0.655 | 0.702 | 0.067 | 0.077 |
| Mallacoota | 29 | 7 | 0 | 5.949 | 0.552 | 0.632 | 0.128 | 0.088 |
| Tasmania | 34 | 7 | 0 | 6.148 | 0.647 | 0.713 | 0.094 | **0.033** |
| Tasmania (Ot2) | 23 | 7 | 0 | 5.999 | 0.826 | 0.700 | -0.184 | 0.950 |
| Across sites | 32 | 7.8 | 0 | 6.667 | 0.680 | 0.733 | 0.073 | **0.006** |
| Historical distribution | 87 | 12 | 3 | 11.719 | 0.701 | 0.717 | 0.022 | 0.077 |
| Range extension | 89 | 10 | 1 | 9.902 | 0.663 | 0.790 | 0.161 | **0.013** |
| Ovul02 | | | | | | | | |
| Nambucca Heads | 17 | 19 | 2 | 18.232 | 0.706 | 0.943 | 0.257 | **0.001** |
| Swansea | 30 | 25 | 1 | 19.004 | 0.800 | 0.961 | 0.170 | **0.000** |
| Merimbula | 29 | 26 | 1 | 19.197 | 0.828 | 0.954 | 0.135 | 0.088 |
| Mallacoota | 29 | 23 | 2 | 17.661 | 0.967 | 0.954 | -0.013 | 0.591 |
| Tasmania | 37 | 26 | 2 | 17.071 | 0.946 | 0.945 | -0.001 | 0.301 |
| Tasmania (Ot2) | 26 | 18 | 1 | 14.846 | 0.923 | 0.931 | 0.009 | 0.217 |
| Across sites | 33.8 | 24.6 | 1.8 | 18.094 | 0.847 | 0.950 | 0.110 | **0.001** |
| Historical distribution | 89 | 36 | 8 | 35.322 | 0.753 | 0.951 | 0.210 | **0.000** |
| Range extension | 96 | 33 | 6 | 31.351 | 0.938 | 0.943 | 0.006 | 0.382 |
| Ovul05 | | | | | | | | |
| Nambucca Heads | 16 | 3 | 0 | 3.000 | 0.063 | 0.123 | 0.500 | **0.033** |
| Swansea | 30 | 8 | 2 | 5.664 | 0.267 | 0.358 | 0.259 | **0.008** |
| Merimbula | 29 | 7 | 0 | 5.260 | 0.414 | 0.414 | 0.000 | 0.588 |
| Mallacoota | 29 | 7 | 2 | 5.065 | 0.241 | 0.287 | 0.161 | 0.051 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Tasmania | 35 | 7 | 1 | 4.882 | 0.629 | 0.503 | -0.255 | 1.000 |
| Tasmania (Ot2) | 26 | 6 | 0 | 5.036 | 0.692 | 0.578 | -0.203 | 0.969 |
| Across sites | 33 | 7.2 | 1 | 4.976 | 0.328 | 0.382 | 0.204 | **0.010** |
| Historical distribution | 88 | 12 | 3 | 11.663 | 0.273 | 0.327 | 0.167 | **0.005** |
| Range extension | 93 | 13 | 4 | 12.418 | 0.505 | 0.632 | 0.201 | **0.001** |
| Ovul08 | | | | | | | | |
| Nambucca Heads | 17 | 4 | 0 | 3.882 | 0.271 | 0.294 | -0.088 | 1.000 |
| Swansea | 30 | 4 | 0 | 3.801 | 0.333 | 0.351 | 0.051 | 0.446 |
| Merimbula | 29 | 4 | 0 | 3.875 | 0.345 | 0.387 | 0.110 | 0.283 |
| Mallacoota | 29 | 6 | 1 | 4.738 | 0.345 | 0.313 | -0.102 | 1.000 |
| Tasmania | 34 | 4 | 0 | 3.193 | 0.382 | 0.328 | -0.169 | 1.000 |
| Tasmania (Ot2) | 23 | 6 | 1 | 5.342 | 0.522 | 0.474 | -0.102 | 0.910 |
| Across sites | 32.4 | 4.8 | 0.4 | 4.118 | 0.347 | 0.347 | -0.031 | 0.795 |
| Historical distribution | 89 | 4 | 0 | 4.000 | 0.337 | 0.343 | 0.017 | 0.416 |
| Range extension | 89 | 7 | 3 | 6.820 | 0.404 | 0.369 | -0.096 | 0.961 |
| Ovul09 | | | | | | | | |
| Nambucca Heads | 16 | 10 | 0 | 10.000 | 0.875 | 0.879 | 0.005 | 0.169 |
| Swansea | 30 | 14 | 1 | 11.249 | 0.867 | 0.892 | 0.029 | 0.184 |
| Merimbula | 29 | 16 | 3 | 12.510 | 0.931 | 0.898 | -0.037 | 0.828 |
| Mallacoota | 29 | 13 | 1 | 11.165 | 0.828 | 0.895 | 0.076 | 0.055 |
| Tasmania | 32 | 15 | 2 | 11.304 | 0.875 | 0.889 | 0.016 | **0.276** |
| Tasmania (Ot2) | 17 | 12 | 0 | 11.702 | 0.706 | 0.891 | 0.213 | **0.051** |
| Across sites | 30.6 | 14.2 | 1.6 | 11.294 | 0.863 | 0.891 | 0.032 | 0.010 |
| Historical distribution | 88 | 20 | 5 | 19.657 | 0.875 | 0.895 | 0.023 | **0.009** |
| Range extension | 81 | 19 | 4 | 19.000 | 0.827 | 0.894 | 0.075 | **0.018** |
| Ovul14 | | | | | | | | |
| Nambucca Heads | 17 | 7 | 0 | 6.882 | 0.706 | 0.824 | 0.147 | **0.080** |
| Swansea | 30 | 8 | 0 | 6.851 | 0.700 | 0.820 | 0.149 | 0.101 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Merimbula | 29 | 6 | 0 | 5.768 | 0.793 | 0.793 | 0.000 | 0.563 |
| Mallacoota | 29 | 9 | 0 | 6.975 | 0.724 | 0.754 | 0.041 | 0.368 |
| Tasmania | 35 | 10 | 1 | 7.916 | 0.800 | 0.810 | 0.013 | **0.518** |
| Tasmania (Ot2) | 26 | 10 | 3 | 8.300 | 0.692 | 0.837 | 0.176 | **0.003** |
| Across sites | 33.2 | 8.8 | 0.8 | 6.949 | 0.735 | 0.804 | 0.086 | **0.002** |
| Historical distribution | 89 | 9 | 0 | 8.813 | 0.730 | 0.803 | 0.091 | 0.071 |
| Range extension | 93 | 16 | 6 | 15.204 | 0.742 | 0.813 | 0.087 | **0.003** |
| Ovul16 | | | | | | | | |
| Nambucca Heads | 17 | 2 | 0 | 2.000 | 0.176 | 0.166 | -0.067 | 1.000 |
| Swansea | 30 | 4 | 1 | 3.523 | 0.367 | 0.395 | 0.073 | 0.207 |
| Merimbula | 29 | 4 | 0 | 3.544 | 0.379 | 0.406 | 0.067 | 0.421 |
| Mallacoota | 29 | 4 | 0 | 3.515 | 0.400 | 0.487 | 0.181 | 0.056 |
| Tasmania | 37 | 5 | 2 | 3.794 | 0.405 | 0.384 | -0.057 | **0.025** |
| Tasmania (Ot2) | 25 | 4 | 2 | 3.473 | 0.120 | 0.224 | 0.471 | **0.025** |
| Across sites | 33.6 | 4.2 | 1 | 3.317 | 0.323 | 0.356 | 0.072 | **0.000** |
| Historical distribution | 89 | 5 | 2 | 4.910 | 0.326 | 0.349 | 0.067 | 0.304 |
| Range extension | 95 | 8 | 5 | 7.534 | 0.316 | 0.373 | 0.155 | **0.000** |

*n*, number of individuals genotyped; $N_A$, number of alleles; $N_{PA}$, number of private alleles; $A_R$, allelic richness; $H_O$, observed heterozygosity; $H_E$, expected heterozygosity; $F_{IS}$, Fixation index; P value, probability for deviation from Hardy-Weinberg equilibrium (Significant values are indicated in bold). Historic distribution zone: Nambucca Heads, Swansea, Ulladulla, Merimbula, and Eden at New South Wales. Range extension zone: Mallacoota, and Cape Conran at Victoria, north-eastern Tasmania. The common group Ot1 indicated in the text is comprised of individuals from all sites. The distinct group Ot2 is predominately comprised of individuals from Tasmania (red cluster in figures 4.1 and 4.2). Descriptive statistics are not shown for Ulladulla, Eden and Cape Conran given their small number of samples ($n$ <17)

Rodhouse PGK, Pierce GJ, Nichols OC, Sauer WHH, Arkhipkin AI, Laptikhovsky VV, Lipinski MR, Ramos JE, Gras M, Kidokoro H, Sadayasu K, Pereira J, Lefkaditou E, Pita C, Gasalla M, Haimovici M, Sakai M, Downey N (2014) Environmental effects on Cephalopod population dynamics: Implications for management of fisheries. In: Advances in Marine Biology. Advances in Cephalopod Science: Biology, Ecology, Cultivation and Fisheries. Vol. 67, Vidal EAG (editor). pp 140–145. Academic Press, London



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# Body Size, Growth and Life Span: Implications for the Polewards Range Shift of *Octopus tetricus* in South-Eastern Australia

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## Abstract

Understanding the response of any species to climate change can be challenging. However, in short-lived species the faster turnover of generations may facilitate the examination of responses associated with longer-term environmental change. *Octopus tetricus*, a commercially important species, has undergone a recent polewards range shift in the coastal waters of south-eastern Australia, thought to be associated with the southerly extension of the warm East Australian Current. At the cooler temperatures of a polewards distribution limit, growth of a species could be slower, potentially leading to a bigger body size and resulting in a slower population turnover, affecting population viability at the extreme of the distribution. Growth rates, body size, and life span of *O. tetricus* were examined at the leading edge of a polewards range shift in Tasmanian waters (40°S and 147°E) throughout 2011. *Octopus tetricus* had a relatively small body size and short lifespan of approximately 11 months that, despite cooler temperatures, would allow a high rate of population turnover and may facilitate the population increase necessary for successful establishment in the new extended area of the range. Temperature, food availability and gender appear to influence growth rate. Individuals that hatched during cooler and more productive conditions, but grew during warming conditions, exhibited faster growth rates and reached smaller body sizes than individuals that hatched into warmer waters but grew during cooling conditions. This study suggests that fast growth, small body size and associated rapid population turnover may facilitate the range shift of *O. tetricus* into Tasmanian waters.

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## Introduction

The distribution and abundance of marine species depends on their functional traits and associated biotic factors, i.e. population genetic structure and gene flow [1], physiological limits [2–4], phenotypic plasticity [5], dispersal ability [6,7], and intra and inter-specific interactions [8,9]. These functional traits and biotic factors are in turn modulated by abiotic factors such as temperature, oxygen and pH [2,10]. Temperature is by far the easiest abiotic factor to record and therefore the most studied environmental variable. Moreover, all aspects of ectotherm behaviour and physiology are sensitive to environmental temperature [11], and species changes in distribution in response to climate change are thought to be largely driven by fluctuations in temperature [12]. However, there are substantial inter-specific differences in the magnitude of responses to such temperature variability [4], and we have little knowledge about the processes responsible for the vast variation in species responses. Some studies have suggested that in response to ocean warming, marine species with short lifespans, high genetic diversity, high dispersal capacity, e.g. with a planktonic larval stage or high migration potential, and that live near their upper thermal limit may be more able to change their distribution as they track their optimum thermal conditions [4,11,13,14].

Long-term data sets appropriate to examine the response in life history parameters of long-lived species that may be undergoing climate-driven range shifts are rarely available [15]. In contrast, ecologically and commercially important cephalopods [16] may facilitate the examination of such life history parameters as a function of their generally short lifespan [17]. Life histories of cephalopods are extremely flexible under changing environmental conditions [18], largely due to the effect of temperature on growth [19], size at maturity [20], hatchling size [21], as well as social and behavioural aspects of courtship, mating, and egg-laying [22]. The combination of temperature-driven flexibility in life-history and the short lifespan of cephalopods may be critical for their capacity to thrive under ocean warming.

The gloomy or common Sydney octopus, *Octopus tetricus*, is a merobenthic species with a planktonic paralarval stage of 2.2±0.01 SE mm at hatching size (Ramos et al. unpublished data) that is subjected to ocean currents. The duration of the paralarval stage before settlement is unknown for *O. tetricus* but it is assumed to be similar to that of closely related species [23], i.e.

35–60 days for *O. vulgaris* reared under laboratory conditions [24,25]. *Octopus tetricus* reaches an approximate arm-span of 2 m [26,27]. This species is commonly distributed in temperate waters of the east coast of mainland Australia, from southern Queensland to southern New South Wales as suggested by scientific surveys [27,28]. However, its distribution has extended polewards to south-eastern Australia, along the coasts of Victoria (see [29]) after 2000 approximately, and eastern Tasmania in 2006 (as reported by fisheries data [30] and supported by citizen science monitoring using scientist-verified and geo-referenced photographs [31,32]; Fig. 1). This polewards shift in distribution, like many others in the same area (e.g. see [32,33]), is thought to be related to the southern extension of the warm East Australian Current (EAC) [34,35] and is consistent with expected changes in distribution promoted by climate driven warming [12]. The EAC flows from the southern Coral Sea and reaches the south-east coast of mainland Australia [36]. Over the past 60 years the EAC has extended approximately 350 km further south, along the relatively cool east coast of Tasmania [34,35]. This extension of the EAC has resulted in the southern Tasman Sea warming at a rate of three to four times the global average, with the ocean temperatures in the region projected to increase by 3°C by 2070 [37].

Like other cephalopods that are key components of trophic webs [16], *O. tetricus* may play an important ecological role in transition of the energy flux from low to high trophic levels. For example, by competing with other octopus species for ecologically and commercially important prey species [38–40]. Furthermore, *O. tetricus* is an important target of the octopus fishery in its historical distribution [26] and now also in the leading edge of its range extension, contributing 14% of the octopus catch. Thus, *O. tetricus* provides a good opportunity to examine the influence of environmental variability on life history characteristics, in particular growth, body size and lifespan; and how such characteristics may influence its capacity to become established in the new sections of its range, i.e. if growth rate and population turnover are fast, the establishment of the population will be favoured in the range extension.

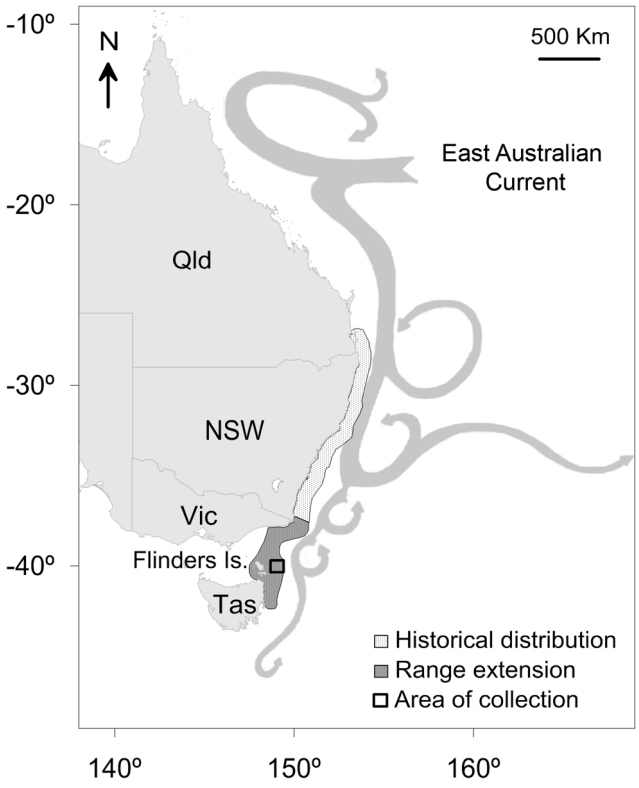


**Figure 1. Distribution of *Octopus tetricus* along the east coast of Australia.** Collection site off eastern Flinders Island at north-eastern Tasmania, Australia during 2011; Qld = Queensland; NSW = New South Wales; Vic = Victoria; Tas = Tasmania.
doi:10.1371/journal.pone.0103480.g001

Therefore, this study aims to examine the effect of environmental variables on the life history characteristics of *O. tetricus* at the southern edge of the recent range shift, in particular the size structure, growth rates and lifespan, and discuss how these characteristics may potentially influence the current and future establishment of this species in Tasmanian waters.

## Materials and Methods

### Ethics statement

This research was conducted under the University of Tasmania Animal Ethics Committee, permit approval no. A11591. No specific collection permits were required given that *Octopus tetricus* is not an endangered or protected species, and specimens were provided by commercial fishers.

### Collection of wild caught specimens

Octopuses were collected by fishers using black plastic shelter pots, 0.3-m long ×0.1-m high ×0.1-m wide, laid on the seafloor at a depth of 35–46 m off the east coast of Flinders Island, north-eastern Tasmania (approximately 40°S and 147°E; Fig. 1) during January (n = 47), February (n = 78), April (n = 93), May (n = 92), July (n = 45), September (n = 76) and December (n = 96) 2011 on board of the commercial *FV Farquharson*.

The whole animals were frozen on board at −20°C. Specimens collected during February and May 2011 were preserved on board in 80% ethanol. Individuals were dissected in the laboratory and eviscerated total wet weight (TW) and mantle weight (MW) (g) were recorded. Mantle weight was preferred over TW because missing and incomplete arms from many individuals provided an underestimate of TW. However, TW was recorded to facilitate comparison with previous studies. Measurements and weights were recorded to the nearest 0.1 cm and 0.01 g respectively.

To correct weights of −20°C frozen and 80% ethanol preserved individuals, sections of mantle tissue of 1 cm width ×2 cm length of different wild caught individuals were weighed fresh and frozen at −20°C (n = 100) or preserved in 80% ethanol (n = 86). Weight was recorded again after the same period of time that passed between collection of wild caught specimens and weighing in the lab.

Sex and maturity (immature, mature and spent) were determined based on the macroscopic characteristics of the gonads. The maturity scale was modified from previous studies [41,42].

### Age estimation

Stylets, the vestigial shells of octopods, have recently been used with success to estimate age and growth rates [43–48]. Stylets were removed from the mantle of fresh, frozen or 80% ethanol preserved specimens and stored in 70% ethanol. Stylets of all specimens (n = 527) were cut, embedded, ground, and polished following [46] with slight modifications: Two to five pictures, depending on section diameter, were sequentially taken from the nucleus to the edge of the section at either ×100, ×200 or ×400 magnification (Fig. 2) using the software Leica Application Suite (LAS) v. 3.6.0 (Leica Microsystems, Switzerland) with a transmit-

ted-light microscope Leica DM LB2 connected to a digital camera Leica DFC420. Pictures were sequentially stitched together and daily increments identified following [43]. Two non-consecutive increment counts were made by one reader using key counter software (KeyCounter v. 1.1.0) and a third count was carried out by a second reader. Recorded number of growth increments was considered as the mean of the three counts. Stylet sections were discarded (n = 313) if growth increments were not clear along the section, if more than 10% of the section was unable to be counted, and if the three counts differed by more than 10%. The daily periodicity of growth increments was assumed in this study as it has been validated or assumed for holobenthic [43] and merobenthic octopods [46–48].

## Oceanographic data

Monthly average Sea Surface Temperature (SST) and Chlorophyll-*a* (Chl-*a*) concentration of the sampling area was obtained from the MODISA satellite imagery at a 4 km scale (http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/Monthly/4 km/). Sea surface temperature was considered a valid temperature estimate of the habitats occupied by *Octopus tetricus* because this species was collected at shallow depths (35–46 m) where wind driven mixing is high and tidal currents are strong [49]. Chlorophyll-*a* concentration is an estimator of primary productivity often with strong links to the abundance of higher trophic levels [50,51].

## Data analyses

Paired sample t-tests were used to assess significant differences between fresh and frozen, and fresh and 80% ethanol preserved samples. Model II linear regressions were conducted when necessary to adjust frozen and 80% ethanol weights so they were comparable to fresh weights. All data was Box-Cox transformed when necessary using the "car" package in R v. 3.0.1 [52,53]. Normality was determined using Shapiro-Wilk's test and homogeneity of variances evaluated by visual inspection of residual plots.

Hatch month of each individual was back-calculated, by subtracting an individuals estimated age (days) from its date of capture. Hatch months were grouped into a 'warm season' including December to May (17.6±0.38°C SE and 0.70±0.04 mg $m^{-3}$ SE, n = 12) and a 'cool season' of June to November (13.2±0.30°C SE and 0.90±0.07 mg $m^{-3}$ SE, n = 12) (following [54]). Maximum life span was considered a proxy of population turnover.

The Gompertz, exponential, power and linear growth models were generated for mantle weight of females and males pooled by season of hatching. The 3-parameter Gompertz growth model had the smallest Akaike Information Criterion (AIC) and Akaike weight (wAIC) closest to 1 [55,56] using the package "qpcR" in R v. 3.0.1 [53,57] and was identified as the model that best fitted the size (MW) at age data (Table 1). The Gompertz growth model was constructed using the non-linear weighted least square method following [58]:

$$m(a) = m_\infty e^{-\gamma \exp(-g_1 a)}$$

Where

$$\gamma = \frac{\ln m_2 - \ln m_1}{1 - e^{-g_1 a_2}}, \qquad m_\infty = m_0 e^{\gamma},$$

$$\mu = m_\infty e^{-1}, \qquad SE_\mu = \sqrt{SE_{m_\infty}{}^2 (e^{-1})^2},$$

Where $m$ is mantle weight (g); $a$ is age (days); $m_\infty$ is the asymptote parameter in $m(a)$ (g); $\gamma$ is the shape parameter in $m(a)$; $g_1$ is the rate coefficient parameter in $m(a)$ ($day^{-1}$); $m_1$ and $m_2$ are location parameters in $m(a)$ (g), or predicted mantle weight at minimum or maximum observed age; $a_2$ is the maximum observed age; $\mu$ is the inflection point parameter in $m(a)$ (g) and SE is the standard error. The three parameters to estimate are $m_\infty$, $\gamma$ and $g_1$. The 95% confidence intervals for the coefficients of the Gompertz growth model were estimated by bootstrapping using the package "car" in R v. 3.0.1 [52,53]. The F-statistics was calculated through an analysis of residual sum of squares (ARSS) to compare Gompertz growth models between genders and among warm and cool hatching seasons [59]. The instantaneous relative rate of growth ($G$) for the Gompertz model was estimated following [58]:

$$G = \hat{\gamma}\hat{g}_1 e^{-g_1 a}$$

A two-way ANOVA was used to compare differences in MW of mature females, and mature and spent males, as well as to compare differences in age of mature and spent females and mature and spent males among warm and cool seasons of hatching. All statistics and models were carried out using R v. 3.0.1 [53].

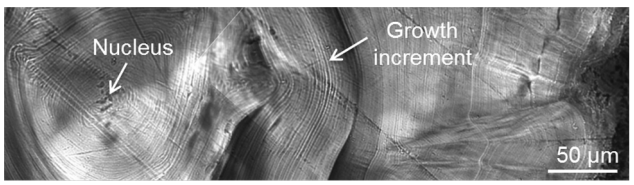


**Figure 2. Stylet of *Octopus tetricus*.** Microstructure of a stylet's transverse section where growth increments are observed.
doi:10.1371/journal.pone.0103480.g002

# Results

## Body size and life span

A total of 527 *Octopus tetricus* (250 females and 277 males) were collected during 2011, approximately 40% of which were smaller than 40 g in MW. Mantle weight distribution was not significantly different between females (5–209 g) and males (3–189 g, Fig. 3) (ANOVA, $F_{(1,505)} = 0.338$, $P > 0.56$); with TW ranging between 60–2260 g for females and 50–2100 g for males. Age of females was not significantly different from age of males (ANOVA, $F_{(1,212)} = 0.039$, $P = 0.84$); females were estimated to be 85–308 days (n = 103) of age and males 88–313 days (n = 111, Fig. 3). Maximum life span was 11 months.

## Growth rates, body size and life span at hatch seasons

Individuals collected in 2011 hatched throughout 2010 and 2011. Greatest numbers of these animals hatched in 2010 when SST was at coolest and Chl-*a* concentration highest (Fig. 4). A second hatching peak was observed in January 2011 when SST was increasing and Chl-*a* concentration was decreasing. The estimated average instantaneous relative growth rate $\left(\hat{G}\right)$ of all *O. tetricus* in north-eastern Tasmania was 0.014±0.0006 SE $day^{-1}$, n = 214 (Table 2). The ARSS indicated that growth models

**Table 1.** Akaike Information Criterion (AIC) and Akaike weight (wAIC) for each growth model fitted to mantle weight at age for *Octopus tetricus* that hatched in warm or cool seasons.

| | Warm | | Cool | |
|---|---|---|---|---|
| **Growth model** | **AIC** | **wAIC** | **AIC** | **wAIC** |
| Gompertz | −3129.39 | 1 | −13709.12 | 1 |
| Exponential | −2615.98 | <0.0001 | −9572.86 | 0 |
| Power | 787.16 | 0 | 1229.35 | 0 |
| Linear | 784.14 | 0 | 1219.75 | 0 |

Individuals were collected at north-eastern Tasmania, Australia during 2011.
doi:10.1371/journal.pone.0103480.t001

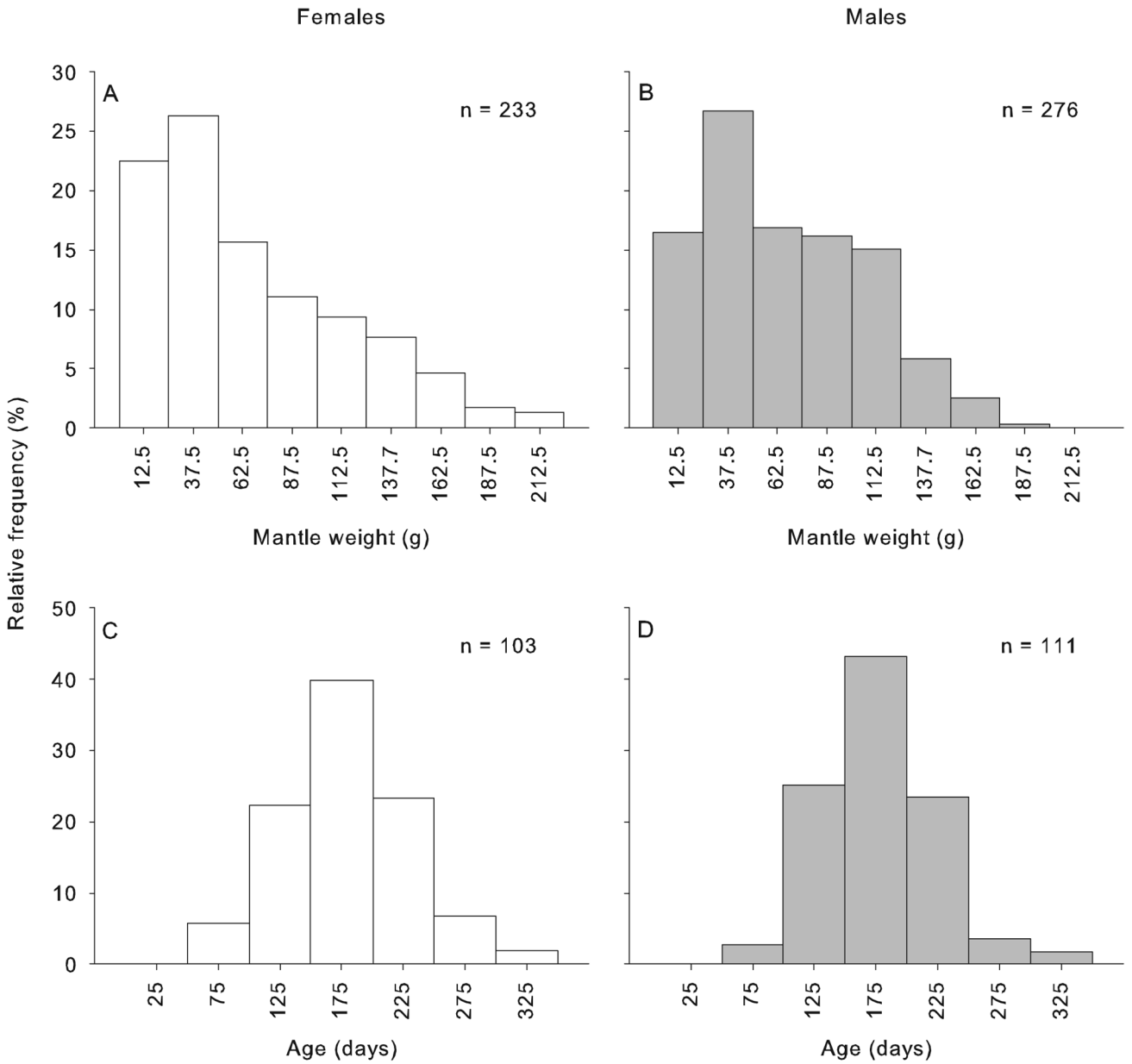


**Figure 3. Relative frequency distribution of females and males *Octopus tetricus*.** Relative frequency (%) at A–B) mantle weight (g) and C–D) age (days), respectively at the range extension off north-eastern Tasmania, Australia during 2011.
doi:10.1371/journal.pone.0103480.g003

differed between hatching seasons ($F_{(3,211)} = 7.03$, $P<0.0001$; Fig. 5). For instance, instantaneous relative growth rate of cool hatched animals was significantly faster than the instantaneous relative growth rate of warm hatched animals (Table 2). Growth models differed only between females and males that hatched in the warm season ($F_{(3,77)} = 2.79$, $P<0.0001$).

Approximately 14% of captured females and 44% of captured males were mature or spent. Maximum MW of mature females was significantly different between hatching seasons (ANOVA, $F_{(1,10)} = 13.2$, $P = 0.005$), with females that hatched during the warm season heavier (144.89±8.56 SE g, n = 5) than females that hatched in the cool season (94.92±9.83 SE g, n = 7). Similarly, mature and spent males that hatched in the warm season were heavier (120.28±7.24 SE g, n = 19) than males that hatched in the cool season (92.20±7.09 SE g, n = 22; ANOVA, $F_{(1,39)} = 7.61$, $P = 0.009$). Considering only mature and spent females, individuals that hatched in the warm season were significantly older (271±11.72 SE days, n = 6) than females that hatched in the cool season (194.75±13.26 SE days, n = 8; ANOVA, $F_{(1,12)} = 17.13$, $P = 0.001$). In contrast, age of mature and spent males that hatched in the warm season (196.32±7.15 SE days, n = 19) did not differ significantly from the age of males that hatched in the cool season (218.32±9.49 SE days, n = 22; ANOVA, $F_{(1,39)} = 3.26$, $P = 0.08$).

## Discussion

This study demonstrates that *Octopus tetricus* has a fast growth rate, small body size and a short lifespan of approximately 11 months, even at the cooler leading edge of its polewards range extension. These characteristics correspond to an *r*-selected life history strategy, which would facilitate the apparent rapid population expansion of this species and assist the 'invasion' into new environments [60,61]. Fast growth rates and short lifespan, combined with successful reproduction, i.e. mating, high fecundity and production of viable embryos (Ramos et al. unpublished data), may underpin a capacity for *O. tetricus* to quickly increase the size of the emerging population in the zone of the range extension. Additionally, such a short lifespan and associated high population turnover may give *O. tetricus*, most likely an efficient generalist predator at the population level like most other octopus species [62,63], a competitive advantage in the short term (see [64]) over the longer-lived species already found within the new range area.

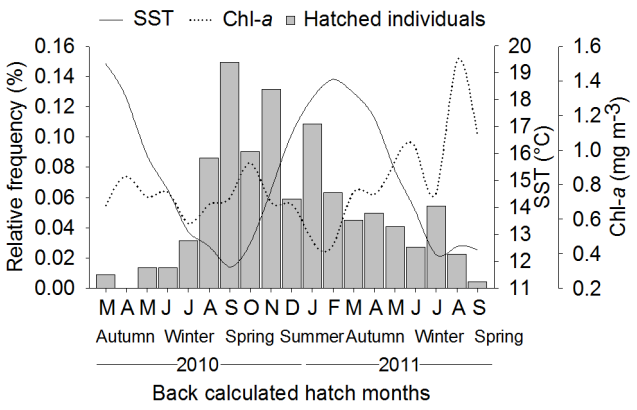


**Figure 4. Relative frequency (%) of hatched *Octopus tetricus* (n = 214) from north-eastern Tasmania, Australia during 2011.** Warm months are indicated in bold and cool months are indicated in italic.
doi:10.1371/journal.pone.0103480.g004

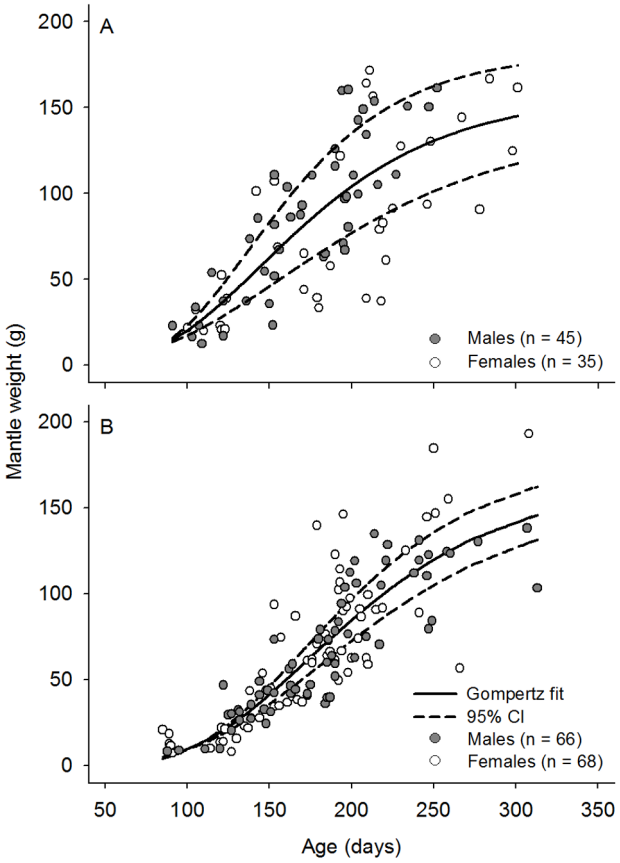


**Figure 5. Growth of *Octopus tetricus*.** Mantle weight (g) and age (days) data, and fitted 3-parameter Gompertz growth model for *Octopus tetricus* that hatched in A) warm and B) cool seasons at north-eastern Tasmania, Australia. Individuals were collected during 2011 and hatch seasons were back-calculated from growth increments in stylets. CI = Confidence interval.
doi:10.1371/journal.pone.0103480.g005

If food supply is not limited, octopuses from cooler waters are expected to grow slower during the exponential phase of growth and reach maturity at larger sizes compared to octopuses from warmer waters [65,66]. In contrast, most individuals collected in the relatively cooler Tasmanian waters during 2011 (annual average 15.3±2.4°C SD, n = 12 months), were quite small (< approx. 400 g TW) with the maximum of 2.3 kg TW measured, compared with larger individuals (>3 kg of TW, S. Montgomery pers comm) reported from the warmer New South Wales waters (annual average 20.3±2°C SD, n = 12 months). Life history characteristics, i.e. growth rates, body size and life span, may differ over the distribution of a species, and may even diverge at the extension of the species distribution [61] possibly a function of reduced genetic diversity [67], or altered as an adjustment to the new physical environment [11], or to different community interactions [68]. For example, body size may be smaller in the region of range extension even though life-history theory predicts body size should be larger in cooler waters. Alternatively, the use of shelter pots may have led to aggregation of mature females or limited the body size of *O. tetricus* collected in Tasmanian waters. In contrast, the use of trawl nets in New South Wales would not lead to aggregation of mature females or limit the body size of captured octopuses. However, additional evidence suggests that the age at sexual maturity (206±26 days SD, n = 214; Ramos et al. unpublished data) and time for egg laying and embryo develop-

**Table 2.** Parameter estimates for the 3-parameter Gompertz growth model fitted to mantle weight at age, and instantaneous relative growth rate for backed calculated hatched *Octopus tetricus* from north-eastern Tasmania, Australia collected during 2011.

| By hatch season | n | Age (days) | $\hat{\mu}$ (g) | $\hat{\gamma}$ | $\hat{g}_1$ (day$^{-1}$) | $\hat{G}$ (day$^{-1}$) |
|---|---|---|---|---|---|---|
| w | 80 | 91–301 | 57.90 (4.93) | 10.15 (2.50) | 0.016 (0.0023) | 0.012 (0.001) |
| c | 134 | 85–313 | 61.06 (2.88) | 12.20 (1.52) | 0.015 (0.0009) | 0.016 (0.0009) |
| By gender | | | | | | |
| f | 103 | 85–308 | 88.77 (13.91) | 7.05 (0.76) | 0.009 (0.001) | 0.013 (0.0006) |
| m | 111 | 88–313 | 54.67 (1.09) | 13.77 (1.19) | 0.017 (0.0007) | 0.014 (0.001) |
| All | 214 | 85–313 | 63.11 (3.54) | 9.81 (1.03) | 0.0137 (0.0009) | 0.014 (0.0006) |

$\hat{\mu}$ = inflection point parameter in mantle weight (age) (g); $\hat{\gamma}$ = shape parameter in mantle weight (age) (g); $\hat{g}_1$ = rate coefficient parameter in mantle weight (age) (day$^{-1}$); $\hat{G}$ = instantaneous relative growth rate (day$^{-1}$); c = cool; w = warm; f = females; m = males. Asymptotic standard errors indicated in parenthesis. Significance for estimated parameters $P<0.05$.

doi:10.1371/journal.pone.0103480.t002

ment in Tasmania (~60 days; unpublished data) fits within the estimated life span (~11 months) of *O. tetricus*. So it is likely that a reasonable size range has been measured and maximum body size and life span has not been underestimated in the range extension. This is further supported by the similar lifespan of other merobenthic octopods, e.g. *O. cyanea* (11 months [48]), *O. vulgaris* (12–15 months [69–71]), or *O. bimaculoides* (14 months [65]).

A short lifespan can facilitate rapid population turnover. Selection acts on biological traits of every generation [72]; thus, favoured genotypes are likely to be selected more often in species with shorter generation times [73,74] due to greater probability of occurrence of mutations or formation of new gene complexes [75]. In this sense, it is possible that the combined effects of small body size, short life span, and likely rapid adaptation to environmental changes and biotic pressures may allow exploitation of niches, which may facilitate the establishment of *O. tetricus* in the leading edge of the range shift into Tasmanian waters.

The 3-parameter Gompertz growth model was an appropriate fit for size at age of *O. tetricus*. This model has adequately described non-linear relationships for growth estimations for other cephalopods taxa, e.g. squids [58,76], and is simpler than other models, i.e. the 4-parameter Schnute growth model [58]. To our knowledge, this is the first study that suggests the Gompertz model as the best fit for growth of an octopod. Therefore, it is not possible to compare with growth models of other octopods. In contrast, the instantaneous growth rate estimated in this study is comparable only to those estimated during the exponential growth of octopods using the equation ($G = (\ln W_2 - \ln W_1)/(t_2 - t_1)$) by [19,58]. *Octopus tetricus* shows similar growth rates compared to wild caught octopods in their historical distribution, e.g. $0.011 \pm 0.003$ SE day$^{-1}$, n = 628 for *O. vulgaris* [69], and octopods in captivity, e.g. $0.014 \pm 0.0004$ SE day$^{-1}$, n = 18 for *O. pallidus* [77], $0.018 \pm 0.002$ SE day$^{-1}$ for *O. maya*, n~40 [78], and $0.036 \pm 0.005$ SE day$^{-1}$, n = 84 for *O. bimaculoides* [65]. Similarity of growth rates suggests that the growth rate of *O. tetricus* in the area of the range extension may not be negatively impacted, still allowing fast growth rates and promoting a short life span and rapid population turnover. In this sense, fast growth rates may facilitate the establishment of *O. tetricus* at the range extension in Tasmanian waters.

## Influence of environmental factors on growth rates

The estimated frequency of hatched individuals may have been masked by gaps in the collection of specimens during some months, in addition to natural processes such as predation, natural mortality, etc. that were not accounted in this study. With this in mind, our results show that *O. tetricus* hatched throughout the year, with greater number of hatched individuals during the cool and highly productive season. Individuals that hatched in cool and under higher Chl-*a* concentration experienced warming conditions later in their life. Those individuals grew faster and achieved smaller body sizes than individuals that hatched in warm conditions, under low Chl-*a* concentration, and grew during cooling conditions (Fig. 6). Thus, the initial greater peaks of Chl-*a* (and inferred greater availability of food), combined with increasing temperatures after hatching may be related to the faster growth rate of individuals hatched in cool conditions. Similarly, reproductive events of *O. vulgaris* seem to be synchronized with local events of high productivity [79–81] that eventually may benefit hatchlings with greater availability of resources [51]. Likewise, squids have experienced faster growth rates in cool waters and this has been attributed to increased productivity or availability of food (*Todarodes angolensis* [82], *Loliolus noctiluca* [83], *Loligo opalescens* [84]).

Size at age variability was observed as aged increased. Individual growth variability has also been noted in other studies [48,58,71,85]. Such variability in response to environmental factors, particularly to temperature, has been extensively studied in squids [19]. Yet, the relationship of growth in octopods and environmental variability is far from understood [86] and other biological factors such as gender, reproduction, genetics and physiological traits must be considered. For instance, differential growth of females and males has been observed during the slower phase of growth with the start of sexual maturity [19], which may explain the different growth rates observed between females and males that hatched in the warm season. This suggests that SST, availability of food, and probably other environmental and biotic factors influenced growth rates at different levels. Therefore, growth must be studied considering the interaction of environmental and biotic factors, in order to disentangling their individual effects.

This study has provided biological information on age and growth of *O. tetricus* at the leading edge of a recent and rapid range shift. The synchrony of hatching events with environmental conditions, such as availability of higher food concentration and warmer temperatures, appears to have a large influence on growth rates, body size and life span of this octopus. Instantaneous growth rates of *O. tetricus* were similar to those of other octopods within their historical range of distribution or reared in captivity. The estimated life span of 11 months may allow *O. tetricus* to cope with environmental variability and possibly facilitate exploitation of

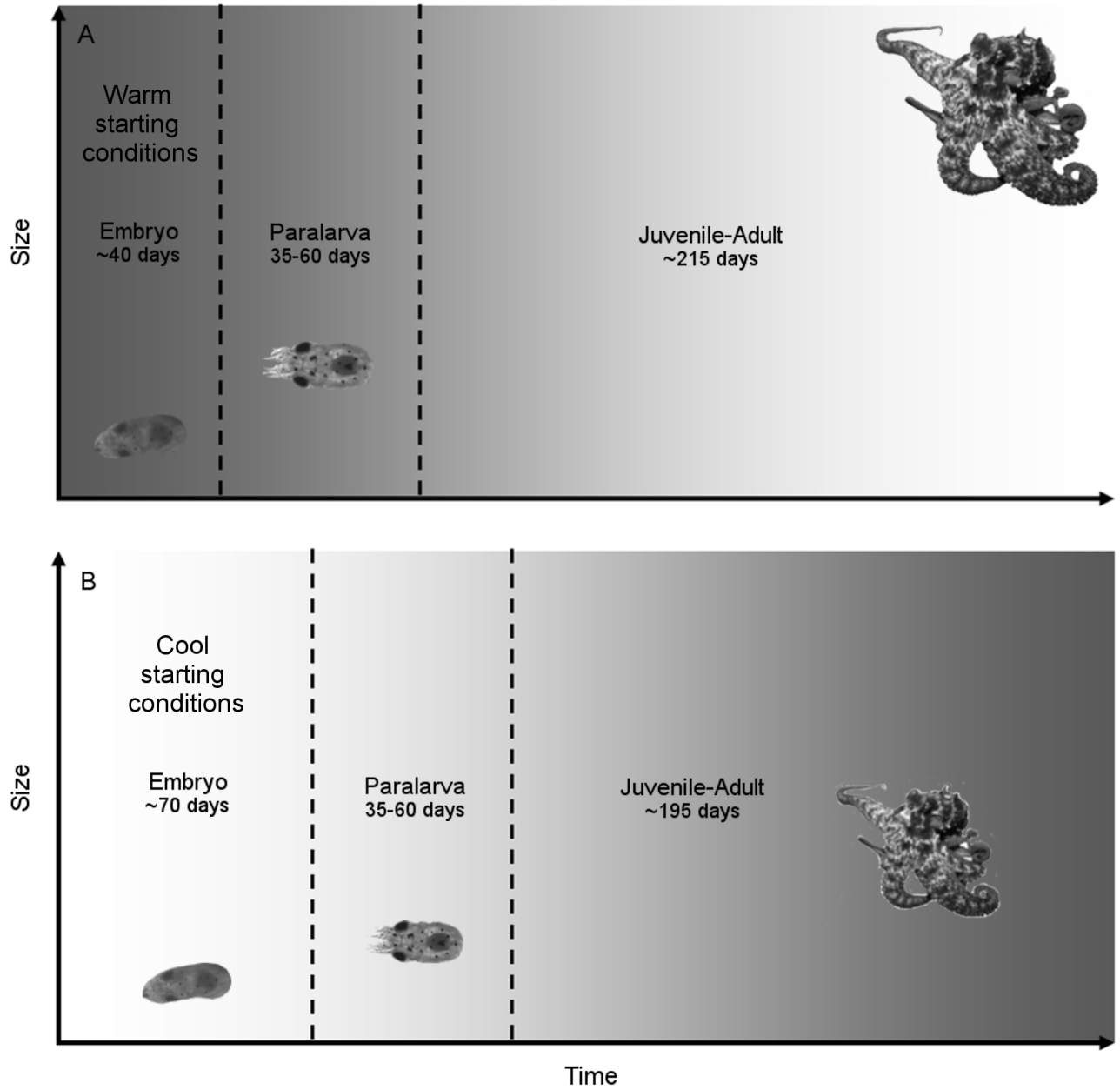


**Figure 6. Life cycle of *Octopus tetricus*.** A) Octopuses that hatch in warm temperatures have a shorter embryonic phase and likely have faster growth during the exponential phase (embryo and paralarva). Decreasing temperatures during the juvenile and adult phases lead to slower growth resulting in longer life span and larger body size. Note the gradient of temperature from warm (dark grey) to cool (light grey). B) Octopuses that hatch in cool temperatures have a longer embryonic phase and slower growth during the exponential phase (embryo and paralarva). Increasing temperatures during the juvenile and adult phases lead to faster growth resulting in shorter life span and smaller body size. Note the gradient of temperature from cool (light grey) to warm (dark grey). Photo of adult *O. tetricus* by Rick Stuart-Smith.
doi:10.1371/journal.pone.0103480.g006

available niches. Additional studies on population linkages, reproductive biology (e.g. Ramos et al. unpublished data), trophic ecology, thermal physiology, and dispersal or migration capacity are essential to develop a more complete understanding of the capacity of a species to alter its range and comprehend the biological and ecological mechanisms that underpin that extension.

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## Author Contributions

Conceived and designed the experiments: JER GTP NAM JM.Strugnell JM.Semmens. Performed the experiments: JER. Analyzed the data: NAM RIL. Contributed reagents/materials/analysis tools: GTP JM.Semmens. Wrote the paper: JER GTP NAM JM.Strugnell JM.Semmens.

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